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Morphological and Phylogenetical Studies in the Isopoda (Crustacea). Part 3: The Pleon Trunk in the Asellota

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With 23 figures

Summary

The skeleton and musculature of the pleon trunk as well as further anatomical characters in basal species of the isopodan group Asellota are described. As far as possible, functional interpretations on the skeletal and muscular systems are proposed. The attempt is made to reconstruct groundpattern characters of the asellotan pleon trunk. The comparison with corresponding morphological data in the taxa Phreatoicidea and Oniscidea indicates character transformations inside the Isopoda. First judgements on the polarity assessment of characters are discussed.

Zusammenfassung

Das Skelet und die Muskulatur des Pleonrumpfes sowie weitere anatomische Merkmale basaler Arten der Isopodengruppe Asellota werden dokumentiert. Soweit dies möglich ist, werden Hypothesen zur Funktion des Skelet-Muskel-Systems vorgeschlagen. Es wird der Versuch unternommen, Grundplan-Merkmale des Pleonrumpfes der Asellota zu rekonstruieren. Der Vergleich mit entsprechenden morphologischen Daten der Taxa Phreatoicidea und Oniscidea weist auf Merkmalstransformationen innerhalb der Isopoda hin. Erste Einschätzungen zur Lesrichtung der Merkmale werden diskutiert.

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1. Introduction

In the first part of the series "Morphological and Phylogenetical Studies in the Isopoda" (ERHARD 1998a) the necessity for detailed descriptions of anatomical characters was emphasized which might be useful to clarify existing inconsistancies in reconstructing the phylogenetic relationships between the main groups of the taxon Isopoda. As a contribution towards a reliable phylogenetical system, investigations on the internal anatomy of isopods are carried out within the scope of the mentioned publication series. While the first and second part (ERHARD 1998a, 1999) deal with the pleonal skeleton and musculature in the Phreatoicidea, the present publication treats the anatomy of the pleon trunk in basal asellotan species. The documented characters of the investigated species are compared with corresponding data of the Phreatoicidea and Oniscidea (ERHARD 1995, 1996, 1997, 1998a, b, 1999). The attempt is made to reconstruct groundpattern characters of the asellotan pleon trunk.

Further parts of the publication series will follow. A fourth part (ERHARD 2001) will describe the pleonal limb morphology in the Asellota and a final fifth paper will

include an analysis of the phylogenetic-systematic relationships between the three isopodan taxa Phreatoicidea, Asellota and Oniscidea.

2. Material, methods and abbreviations

2.1. Material

Tanaidacea

Apseudomorpha

Apseudes latreillii (M. Edwards, 1828), W-France, Brittany, Roscoff.

Isopoda

Asellota

Stenasellus costai Lanza, Chelazzi & Messana, 1970, Somalia, El Ali, (ex coll. MESSANA 322)

Protelsonia gjorgjevici (Racovitza, 1924), Serbia, Paracin, cave Ravanicka (SMNS 5144)

Asellus aquaticus (Linnaeus, 1758), S-Germany, Baden-Württemberg, Tübingen

Vermectias nelladanae Just & Poore, 1992, Australia, Tasmania, Macquarie Island, Green Gorge (ex NMV J21593).

Phreatoicidea

Metaphreatoicus australis (Chilton, 1891), Australia, New South Wales, Mt. Kosciusko (SMNS 14016, 14048)

Colubotelson joyneri searlei Nicholls, 1944, Australia, E-Victoria, Mt. Baw Baw (SMNS 14019)

Onchotelson brevicaudatus (Smith, 1909), Tasmania, Great Lake, southern bank (SMNS 14047)

Mesacanthotelson tasmaniae (Thomson, 1894), Tasmania, Great Lake, southern bank (SMNS 14047)

Paramphisopus palustris (Glauert, 1924), Australia, Western Australia, Lake Monger (SMNS 14119; ex AM P44487)

Phreatoicopsis terricola Spencer & Hall, 1896, Australia, Victoria, The Grampians (SMNS 14118; ex NMV J44869)

Nichollsia kashiensis Chopra & Tiwari, 1950, India, Banaras (SMNS 12149)

Mesamphisopus capensis Barnard, 1914, South Africa, Southern Cape, Zonder End Mountains (SMNS 15517; ex SAM A6052).

Calabozoidea

Calabozoa pellucida Van Lieshout, 1983, Venezuela, Calabozo (ex coll. WÄGELE).

Oniscidea

Ligia oceanica (Linnaeus, 1767), W. France, Brittany, Roscoff

Tylos ponticus Grebnitzky, 1874, Greece, island of Crete, E Sitia and island of Astipalea, Maltesana (SMNS 1242, 1549)

Mesoniscus alpicola (Heller, 1858), S-Germany, Bavaria, 6 km W Berchtesgaden

Titanethes albus Schiödte, 1849, Slovenia, 30 km S Ljubljana, Videm-Popeć, water cave (SMNS 5080, 5253)

Actaecia bipleura Lewis & Green, 1994, Tasmania, W Tamar River, W Greens Beach

Oniscus asellus Linnaeus, 1758, S-Germany, Baden-Württemberg, Tübingen.

Valvifera

Saduria entomon (Linnaeus, 1758), Finland, Tvärminne (SMNS 4205).

"Flabellifera"

Anilocra frontalis Milne-Edwards, 1840, W-France, Brittany, Roscoff.

2.2. Methods

Skeleton and musculature of the pleon trunk were reconstructed by manual micropreparation of fuchsine-stained material under the stereomicroscope and by the use of histological serial sections examined under the light microscope. The thickness of the histological sections was 7 µm, they were stained in haematoxylin-eosin and azan. The skeleton was also investigated after maceration in diethylenetriamine (KRAUTER 1980) and staining in chlorazol-black (CANNON 1937).

The morphological data on the isopodan pleon and further body regions are interpreted, if this is possible at the present state of knowledge, strictly according to the method of phylogenetic systematics proposed by HENNIG (1966).

The morphological study within the paper in hand treats mainly the skleton and musculature of the pleon trunk of the asellotan species *Stenasellus costai, Protelsonia gjorgjevici* (Stenasellidae) and *Asellus aquaticus* (Asellidae). These species of the group Aselloidea were selected because this group might represent the most basal superfamily of the Asellota (cf. KUSSAKIN 1973, WILSON 1987 and WÄGELE 1989). Therefore, it seems to be quite possible that the Aselloidea might still have retained numerous plesiomorphous characters in relation to the asellotan groundpattern.

After the description of one anatomical complex, characters are discussed by in- and outgroup comparisons and attempts are made to reconstruct groundpattern characters of the asellotan pleon trunk. The states of outgroup characters are determined mainly by anatomical investigations of the tanaidacean species *Apseudes latreillii.* Following recently published studies on the phylogeny of the Peracarida (TABACARU & DANIELOPOL 1999, KOBUSCH 1999), the taxon Tanaidacea represents the sistergroup of the Isopoda.

The results were gathered chiefly from male specimens. It is emphasized if females were considered. Within the graphical reconstructions membranes are indicated by bold dotting.

2.3. Abbreviations

A	Point of articulation
AM	Australian Museum, Sydney, Australia
As	Anus
Att	Point of muscular attachment
Con	Connective of the ventral nerve cord
Cox	Pereiopod coxopodite
CoxPlt	Coxal plate
dLM	Dorsal longitudinal musculature
En	Pleopod endopodite
EnDA	Distal article of pleopod endopodite
EnPA	Proximal article of pleopod endopodite
Ex	Pleopod exopodite
ExDA	Distal article of pleopod exopodite
ExPA	Proximal article of pleopod exopodite
Gp	Genital papilla
InMb	Intersegmental membrane
IoPep	Insertion opening of pereiopod
IoPp	Insertion opening of pleopod
M	Muscle
Mm	Muscles
NMV	National Museum of Victoria, Australia
PeDAp	Dorsal apophysis of pereion tergite
PedLMex	External layer of the pereional dorsal longitudinal musculature
PedLMin	Internal layer of the pereional dorsal longitudinal musculature
PeGl	Pereional ganglion of ventral nerve cord
PepBs	Pereiopod basipodite
PepMm	Extrinsic musculature of pereiopod
PeSt	Pereion sternite
PeT	Pereion tergite

PevLMcl Central layer of the pereional ventral longitudinal musculature
PevLMex External layer of the pereional ventral longitudinal musculature
PevLMin Internal layer of the pereional ventral longitudinal musculature
PlDAp Dorsal apophysis of pleon tergite
PlGl Pleonal ganglion of ventral nerve cord
PlSt Pleon sternite
PlT Pleon tergite
PlvLMcl Central layer of the pleonal ventral longitudinal musculature
PlvLMin Internal layer of the pleonal ventral longitudinal musculature
Pp Pleopod
pPrAp Posterior apophysis of pleopod protopodite
Pr Pleopod protopodite
PtScl Ventrocranial pleotelsonic sclerite
PtSt Pleotelson sternite
PtT Pleotelson tergite
SAM South African Museum Cape Town, South Africa
Scl Sclerite
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
Sut Suture
Tend Tendon of connecting tissue
UAp Apophysis of uropod protopodite
UEn Uropod endopodite
UEx Uropod exopodite
UPr Uropod protopodite
Vas Vas deferens
vLM Ventral longitudinal musculature.

In the figures numerous abbreviations are completed by *roman numbers* which apply to corresponding pereion or pleon segments.

3. Previous investigations and terminology

An overview on previous investigations on the pleonal skeleton and musculature in the Isopoda and other peracaridan taxa is given within the first part of the publication series in hand on isopod morphology and phylogenetics (Erhard 1998a: 5). Concerning the special pleonal anatomy of the Asellota, additionally, the following references are worth mentioning: A detailed description of the male pleopods in *Asellus aquaticus* is given by Maercks (1930). Anatomical-phylogenitical studies on the Asellota and subordinate groups are presented by Wägele (1983, 1989), Sket (1985), Wilson (1987, 1991), Schmalfuss (1989) and Brusca & Wilson (1991). Information on external pleonal structures in the groups Vermectiadidae and Stenetriidae are reportet by Just & Poore (1992) and Serov & Wilson (1995).

The results of the present investigation on the pleonal skeleton and musculature of the Asellota will be compared here with literature data of comparative-anatomical studies on the Oniscidea and Phreatoicidea carried out by Erhard (1995, 1996, 1997, 1998a, b, 1999). Therefore, the consecutive numbering of the muscles refers to the nomenclature used in the above cited publications. Gaps in the numbering indicate muscles which are only present in subordinate oniscidean groups (cf. Erhard 1995, 1996, 1997) but not within the groundpattern of the Oniscidea and Phreatoicidea nor in the investigated asellotan species.

For the purpose of consistency, the terms of skeletal structures, their abbreviations and their spellings were adopted from Erhard (1995, 1996, 1997, 1998a, b, 1999).

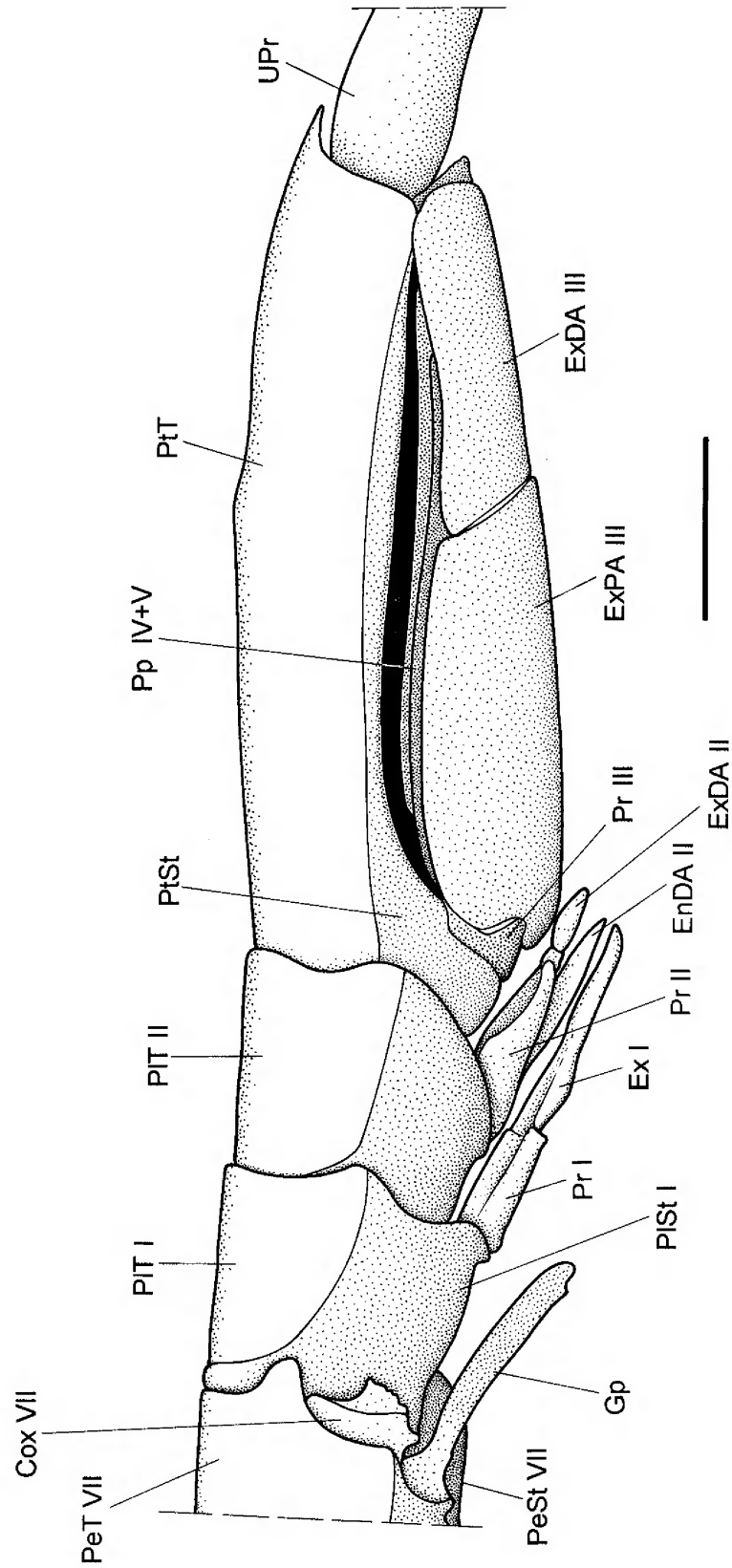


Fig. 1. *Stenasellus costai*, ♂, pleon and pereionite VII in lateral view. Pereiopods VII except for coxopodites removed. – Scale: 1 mm.

4. Skeleton and musculature of the pleon trunk

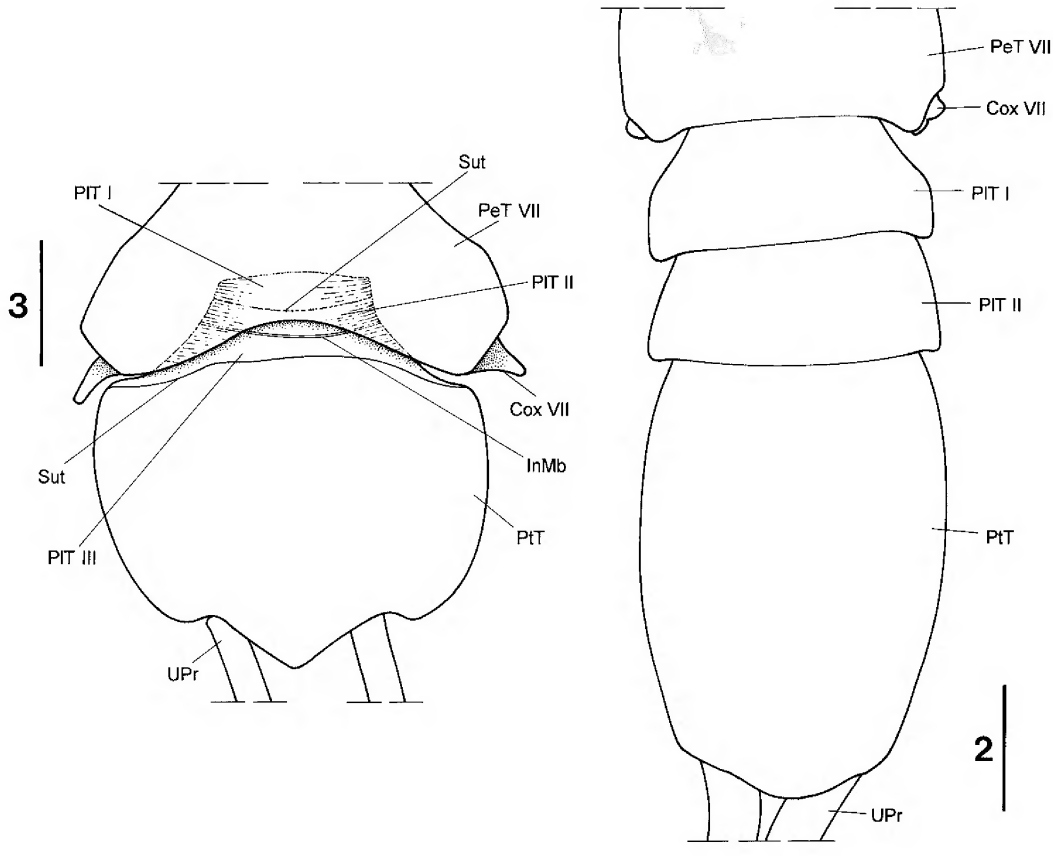
4.1. Skeleton

4.1.1. Exoskeleton (figs. 1–7)

4.1.1.1. Asellotan species

The pleon of *Stenasellus costai* (fig. 1) and *Protelsonia gjorgjevici* consists of the well-developed and freely movable pleon segments I and II and of a large terminal body segment (pleotelson). The latter is formed by the fusion of the pleon segments III–V and the true isopodan pleotelson consisting of the sixth pleon segment and the telson. The pereion segment VII, the pleon segments I and II and the large terminal body segment are connected by intersegmental membranes. No traces of segmental borders between the pleon segments III–V are present at the dorsal side (fig. 2). The ventral border between the pleon segments III and IV of both stenasellid species, however, is still marked by a clearly visible suture but an intersegmental membrane does not occur (fig. 4).

The situation in *Asellus aquaticus* differs from the above described status of *Stenasellus* and *Protelsonia* in respect to the pleon segments I and II which are clearly re-



Figs. 2–3. Pleon and pereionite VII in dorsal view. Pereiopods VII except for coxopodites removed. – 2. *Stenasellus costai*, ♂; – 3. *Asellus aquaticus*, ♂. – Scales: 1 mm.

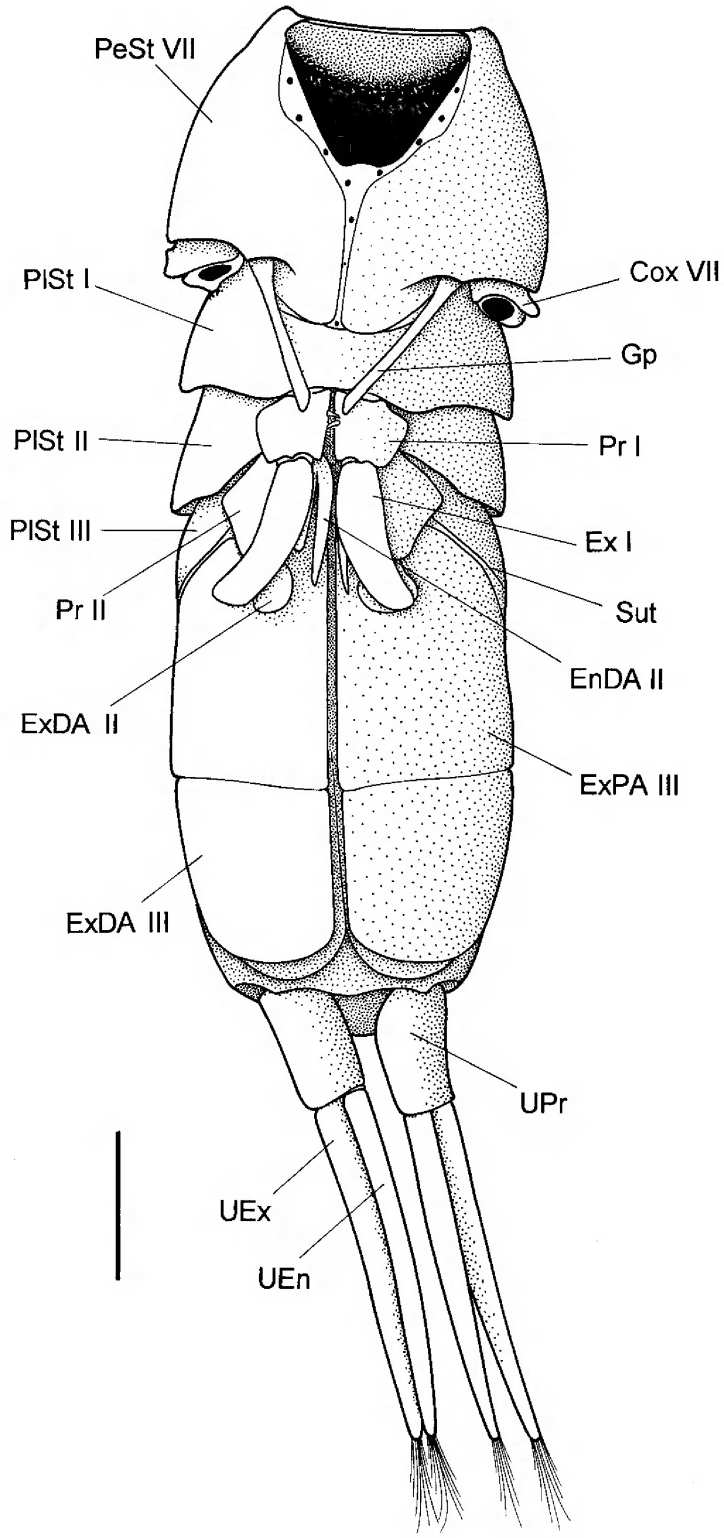


Fig. 4. *Stenasellus costai*, ♂, pleon and pereionite VII in ventral view. Pereiopods VII except for coxopodites removed. – Scale: 1 mm.

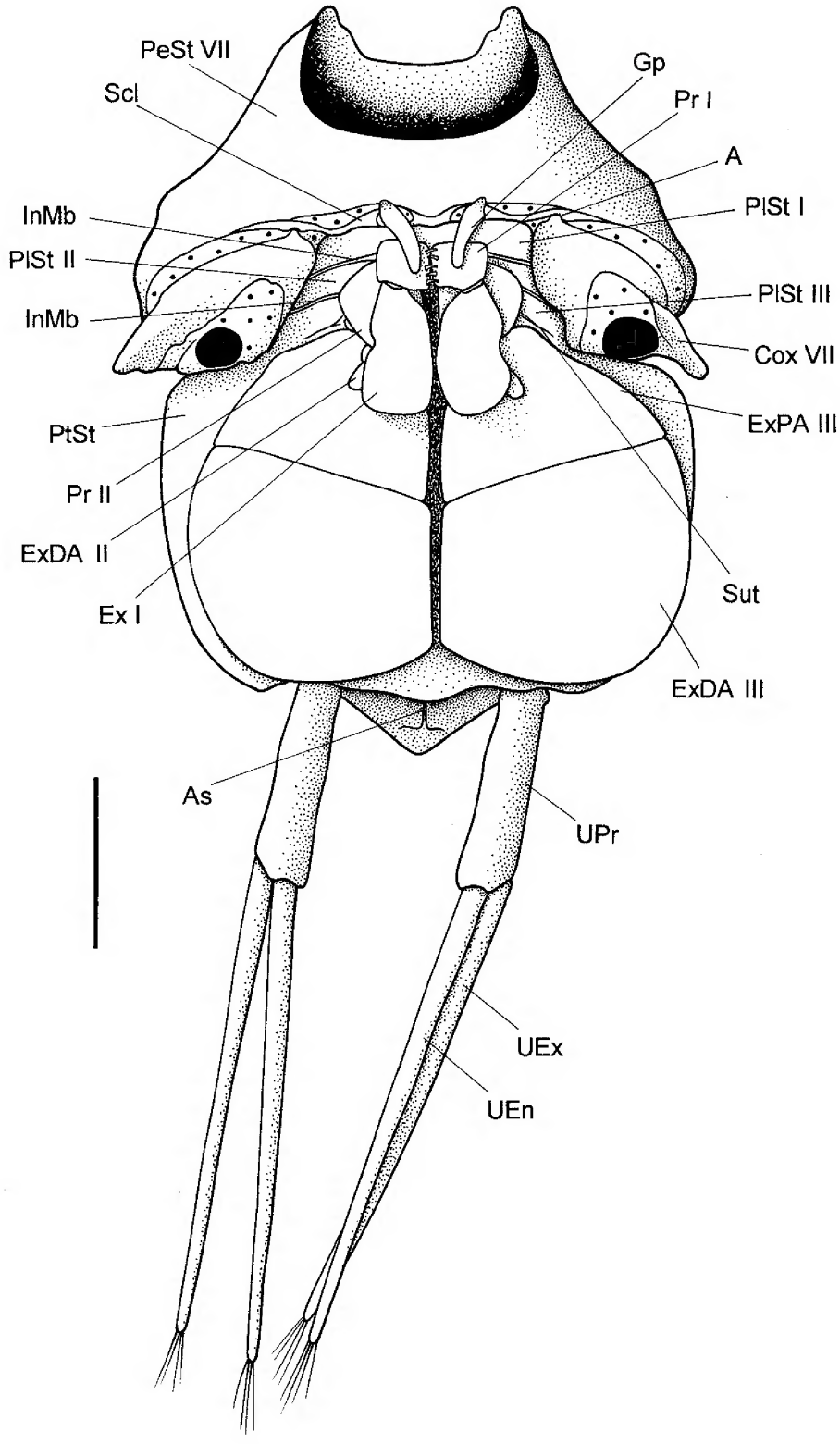


Fig. 5. *Asellus aquaticus*, ♂, pleon and pereionite VII in ventral view. Pereiopods VII except for coxopodites removed. – Scale: 1 mm.

duced in length and partly fused with each other (figs. 3, 5). The intersegmental border between the pleon tergites I and II is still marked by a slight suture only clearly visible in mazerated specimens. This suture is normally covered by the caudal region of the pereion tergite VII (fig. 3). A dorsal intersegmental membrane between pleon tergite I and II obviously is missing but both tergites can easily be separated by manual preparation along the dorsal intersegmental suture.

At the ventral body side, in contrast, a short intersegmental membrane is still present between pleon sternite I and II as well as between pleon sternite II and III (fig. 5).

In contrast to the situation in *Stenasellus costai* and *Protelsonia gjorgjevici* the pleon segment III of *Asellus aquaticus* is dorsally still clearly separated from the large pleotelson by a strong suture which runs along the entire width of the pleon (fig. 3). The presence of this suture gives the impression that the species has retained a free pleon segment III but an intersegmental membrane between pleon tergite III and the terminal pleotelson is missing. At the ventral body side of *Asellus aquaticus* a very short intersegmental membrane is still marking the segmental border between pleon sternite III and the pleotelsonic region (fig. 5). In *Protelsonia* and *Stenasellus* only a ventral suture has been retained at the caudal border of the pleon sternite III (fig. 4).

The pleon of male specimens in *Stenasellus, Protelsonia* and *Asellus* bears five pairs of pleopods and a terminal pair of styliform uropods. Between the uropod protopodites the anus is located in a terminal position. The pleopod I has lost the endopodite while the pleopods II–V are still biramous appendages. The endopodite of the male pleopod II is modified to a copulatory organ. The exopodites of the pleopods III are developed as opercula which are covering the endopodites III and the pleopods IV and V at the ventral pleon side (figs. 4–5). Thus, together with the ventrum of the pleotelson the pleopod exopodites III are forming a protective chamber for the caudal pleopods[1)].

The pleon and especially the pleotelson trunk of *Stenasellus, Protelsonia* and *Asellus* is broader than high and appears slightly compressed dorsoventrally (figs. 1–5). The epimera of the pleon segments and the large pleotelson are either short or absent. Median sternal processus of pleon segments in *Stenasellus* and *Asellus* could only be shown so far between the pleopod protopodites III (cf. ERHARD 2001: figs. 18, 21: StPr).

At each body side a long male genital papilla arises in *Stenasellus costai* and *Protelsonia gjorgjevici* as a cuticular outgrowth from a sclerite of the posterior pereion ventrum VII immediately medially to the articular area of the pereiopod coxopodite VII (figs. 4, 6: Scl). This sclerite, which gives origin to the genital papilla, is clearly separated from the coxopodite VII by a short articular membrane. However, sclerite and coxopodite are forming together the medial articular point of the pereiopod coxopodite VII.

A corresponding sclerite which is bordering the medial articular region of the coxopodite VII is also present in *Asellus aquaticus* (fig. 5: Scl). However, the sclerite extends medially and gives origin to the genital papilla at a position which is distinctly dissociated from the coxopodite VII and located near the midventral longitudinal axis of the pereion ventrum VII.

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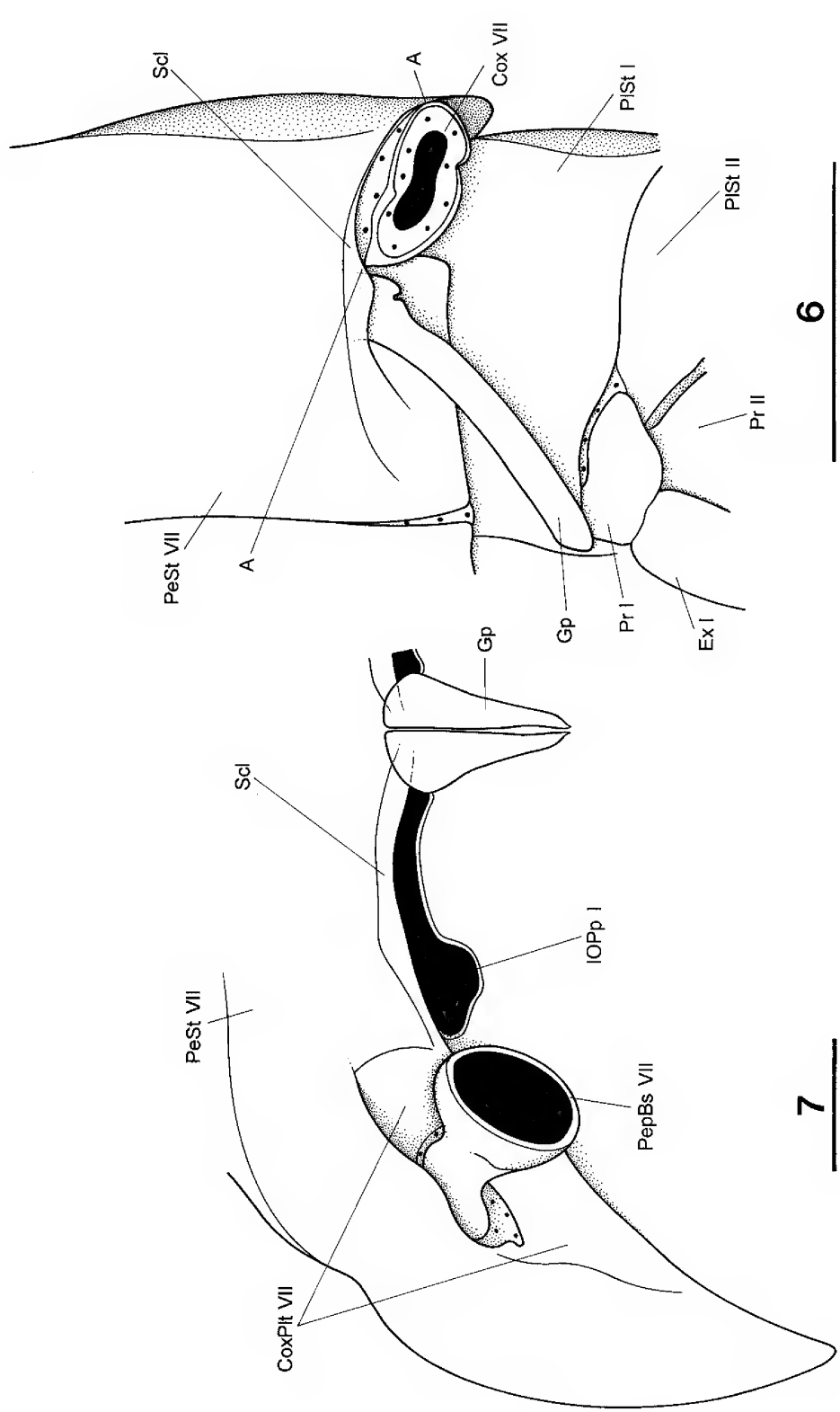
1) The asellotan pleopods and uropods will be treated in detail in the fourth part of the present publication series "Morphological and Phylogenetical Studies in the Isopoda" (ERHARD 2001).



Figs. 6–7. Genital papillae and articular region of pereiopod VII in ventral view. – 6. *Stenasellus costai*, ♂. Pereiopod VII except for coxopodite removed. – 7. *Ligia oceanica*, ♂. Pereiopod VII except for coxo-basipodite articular area removed. – Scales: 1 mm.

4.1.1.2. Comparison

– Pleon segments I and II

The presence of long and well developed pleon segments I and II which are still separated by intersegmental membranes represents a plesiomorphous groundpattern character of the Asellota. This character state is still retained in the asellotan taxon Stenasellidae (figs. 1–2, 4) and probably in the Microcerberidae (cf. WÄGELE 1982, 1983) but it is also present within the groundpatterns of the taxa Phreatoicidea and Oniscidea as well as in further isopodan and peracaridan groups.

The shortening of the pleon segments I and II (e.g. in *Vermectias* and *Asellus,* figs. 3, 5) as well as their partial fusion (e.g. in *Asellus aquaticus*) have to be considered as derived character states of subordinate asellotan groups.

– Free pleonite III and pleotelson

In general it is assumed that the Asellota have only two free pleonites and one large pleotelson formed by the fusion of the pleonites III–VI and the telson (cf. WÄGELE 1989: 60). This status corresponds largely with the situation in *Stenasellus* and *Protelsonia* which lack any dorsal segmental borders between the pleonites III–V (fig. 2). WOLFF (1962) and JUST & POORE (1992), however, reported on asellotan species with three free pleon segments. Actually, the presence of a more or less separate pleon segment III might occur much more frequently as it was supposed to be so far. JUST & POORE (1992) described the external anatomy of the asellotan species *Vermectias nelladanae* and assess the presence of three separate pleon segments as a plesiomorphous feature within the Asellota which might be the right interpretation. However, *Asellus aquaticus* and presumably many more representatives of the Aselloidea and further asellotan superfamilies show nearly the same pleonal tagmata as the adult specimens of *Vermectias nelladanae* (figs. 3, 5; JUST & POORE 1992: fig. 3D). This statement will make sense only then, when the second, dorsally visible pleon segment of *Asellus* is interpreted as the true third pleonite which is dorsally separated by a strong suture and ventrally by an intersegmental membrane from the large pleotelson. This interpretation can hardly verified only by the investigation of the external morphology; the internal structures should also be considered (cf. chapt. 4.1.2.1., fig. 9). The present study of mazerated and stained specimens could clearly show that in *Asellus aquaticus* the pleon tergites I and II are fused forming a uniform segment. Only a very slight suture between the tergites I and II has been retained. However, the pleon sternites I and II as well as the insertion openings of the pleopods I and II are still separated by a short intersegmental membrane. Therefore, at the pleon of *Asellus aquaticus* and, presumably, numerous other asellotan species three instead of two cranial separate segments are distinguishable while the large pleotelson is composed of the pleonites IV–VI and the telson.

Thus, the situation present in *Vermectias* might be not so exceptional as it appears at first sight (cf. JUST & POORE 1992). Only the retention of intersegmental membranes between the pleon tergites I and II as well as between tergite III and the large pleotelson of *Vermectias,* probably might represent a plesiomorphous status in respect to *Asellus aquaticus.* However, the presence of three separate and distinguishable anterior pleon segments represents with all probability a common character of basal asellotan groups which definitely include the genus *Asellus.* On

the other hand, the complete fusion of the pleon segments IV, V and the true isopodan pleotelson (pleonite VI + telson) has to be considered an apomorphous status of the taxon Asellota in respect to the isopodan groundpattern (cf. ERHARD 1998a: 7).

– Shape of the pleotelson

The pleotelsonic trunk in the groundpatterns of the outgroup Tanaidacea, the isopodan taxa *Tainisopus,* Oniscidea, Calabozoidea, Asellota and of most other isopodan groups appear slightly compressed dorsoventrally (fig. 8; VAN LIESHOUT 1983: fig. 1; SIEG 1984: fig. 5; WILSON & PONDER 1992: fig. 1; ERHARD 1995: figs. 2, 13). In contrast, the pleotelsonic trunk in the groundpattern of the Phreatoicidea is voluminous and vaulted (cf. ERHARD 1998a: fig. 1, 1999: fig. 30). Strong pleotelsonic flexors are located within the pleotelson which are partly responsible for the pleotelsonic thrusts the Phreatoicidea are able to perform. As already discussed by ERHARD (1999: 48) this unique type of locomotion and the correlated extraordinary muscular and skeletal development as well as the vaulted pleotelson presumably has to be considered an apomorphous character complex of the Phreatoicidea (cf. WILSON & PONDER 1992: 294; WILSON & KEABLE in press).

– Epimera of the pleon segments

As already discussed by ERHARD (1998a: 7, 37, 1999: 42, 2001) the presence of long downward developed pleon epimera, which are forming parts of a conspicuous ventral pleopodal chamber, has to be considered an apomorphous groundpattern character of the Phreatoicidea. In the presumptive isopodan sistergroup Tanaidacea (cf. TABACARU & DANIELOPOL 1999, KOBUSCH 1999) and in the isopodan taxa Oniscidea, Asellota, *Tainisopus,* Calabozoidea as well as in the remaining isopodan groups comparable structures are missing.

In the asellotan groundpattern the pleopod exopodites III are forming together with the pleotelsonic ventrum a protective chamber for the pleopod endopodites III and the pleopods IV–V (figs. 1, 4, 5, 8, 9; cf. ERHARD 2001). This kind of pleopodal chamber, presumably, represents an apomorphous character state of the Asellota and has been developed independently of the phreatoicidean pleopodal chamber.

– Male genital papillae

Within the isopodan groundpattern the male genital papillae are arising with all probability directly on the medial walls of the pereiopod coxopodites VII (cf. ERHARD 1998a: 38). This plesiomorphous condition is retained within the Isopoda in the Phreatoicidea and in the extraordinary genus *Tainisopus* (cf. WÄGELE 1989; BRUSCA & WILSON 1991, WILSON & PONDER 1992, ERHARD 1998a: 10).

A similar condition shows the asellotan genus *Vermectias.* In male specimens of this group the genital papillae arise from sclerites immediately medial to the coxopodites of the pereiopods VII (cf. JUST & POORE 1992: fig. 6A). A corresponding situation is also present in male specimens of *Stenasellus costai* (fig. 6). This charater state with lateral penes and a short sclerotized bridge between the coxopodite VII and the genital papilla might be the plesiomorphous situation within the taxon Asellota. However, this condition represents an apomorphous character

state in respect to the isopodan and phreatoicidean groundpatterns[2]. In *Asellus aquaticus* the genital papillae arise also from a sclerite which might be homologous to that of *Vermectias* and *Stenasellus* but the genital papillae have been shifted clearly towards the midventral line (fig. 5). According to JUST & POORE (1992: 136) such a medial migration of the genital papillae has occurred independently in more than one subordinate asellotan line, and in advanced forms with fully medial penes no external evidence remains of a sclerite link with the limb base.

In the oniscidean groundpattern the paired male genital papillae are positioned exactly at the midventral longitudinal axis on the posterior margin of the pereion sternite VII (fig. 7; cf. ERHARD 1995: 10). This character state has to be considered as an apomorphous situation in relation to the isopodan, phreatoicidean and asellotan groundpatterns.

In *Ligia oceanica* as well as in all other oniscidean groups the pereiopod coxopodites are modified to coxal plates which are fused with the lateral regions of the pereionites. However, the medially located paired genital papillae of *Ligia* are still arising from a sclerite which might be homologous to that of the basal asellotan species[3]. This sclerite of *Ligia oceanica* extends sidewards and is connected with the "coxal region" of the pereionite VII (fig. 7).

4.1.2. Endoskeleton (figs. 8–9)

4.1.2.1. Asellotan species

The internal anterior edges of the tergites of all pereionites and of the pleonites I–III in *Stenasellus costai* are developed laterodorsally to nose-like apophyses (fig. 8: PlDAp). They are serving as points of attachment for the tergal limb remotors and branches of the longitudinal musculature. According to ERHARD (1995, 1996, 1997, 1998a) these "dorsal apophyses" are also present at all pereional and pleonal tergites within the phreatoicidean and oniscidean groundpattern. However, in the asellotan *Asellus aquaticus* the dorsal apophyses are less developed. Only at the dorsolateral edge of the anterior margin of the pleonite I a conspicuous apophysis is still retained (fig. 9: PlDAp). Dorsal apophyses of the pleon segments IV–VI are completely reduced in *Asellus* as well as in *Stenasellus* and, presumably, in the asellotan groundpattern.

At the posterior internal walls of the pleopod protopodites I–V in *Stenasellus, Protelsonia* and *Asellus* thin apophyses are developed which are projecting into the pleon trunk (figs. 8–9: pPrAp). These apophyses are serving as points of insertion for the tergal pleopod remotors Mm 2, 6, 9, 11, 13 (figs. 11, 19).

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[2] According to WILSON (1994), WILSON & WÄGELE (1994) and ERHARD (1998a: 10) the condition of *Angeliera* and *Microcharon* (Microparasellidae) with male genital papillae attached directly to the coxopodites VII is interpreted so far as a secondary apomorphous status in respect to the asellotan groundpattern caused by a reversion owing to the repositioning of the coxae. Further anatomical investigations are necessary to substantiate or refute this hypothesis.

[3] Within the groundpattern of the Oniscidea the male genital papillae are not arising on the intersegmental membrane between pereionite VII and pleonite I as it was stated by BRUSCA & WILSON (1991: 175), ERHARD (1995: 10) and TABACARU & DANIELOPOL (1999: 169) but on a posterior sclerite of the pereion ventrum VII (fig. 7).

In *Asellus aquaticus* the insertion openings of the pleopods I–V are positioned close together on account of the shortening and fusion of pleonites. In *Stenasellus costai* the pleonites I and II are still developed as long segments (fig. 8). Nevertheless, the insertion openings of the male pleopods I and II are clearly approached, caused by the fact that the pleopod I is inserted at the back margin of pleon sternite I and the pleopod II at the front margin of pleon sternite II.

4.1.2.2. Comparison

– "Dorsal apophyses"
  Dorsal apophyses as points of attachment for longitudinal muscles and the tergal limb locomotors are developed at the anteriolateral edges of the pereional and all pleonal tergites at least in the groundpatterns of the Isopoda, Phreatoicidea, Oniscidea as well as in specimens of the taxa *Saduria* (Valvifera) and *Anilocra* (Flabellifera-Cymothoidae) (cf. ERHARD 1995, 1996, 1997, 1998a). Less developed dorsal apophyses could also be shown in the tanaidacean *Apseudes.* Presumably, as a result of the fusion of the pleon segments IV–VI and the telson in the Asellota (chapt. 4.1.1.2.) as well as the reduction of longitudinal muscles in the caudal pleon trunk (chapt. 4.2.1.) corresponding apophyses within the fused pleon segments IV–VI are completely reduced (figs. 8–9). This situation represents an apomorphous character state of the Asellota in respect to the isopodan groundpattern.

– Protopodal apophyses for the tergal pleopod locomotors
  Within the oniscidean groundpattern (ERHARD 1995, 1996, 1997) and in the investigated asellotan species anterior apophyses at the pleopod protopodites as points of attachment for pleopod promoters are missing (figs. 8–9). In contrast, numerous phreatoicidean species are equipped with anterior protopodite apophyses (ERHARD 1998a) as well as the valviferan species *Saduria entomon* (pleopods IV–V). Posterior pleopod protopodite apophyses as points of attachment for the tergal pleopod remotors Mm 2, 6, 9, 11 and 13 could be shown so far in the Phreatoicidea, Asellota, Oniscidea, Valvifera and "Flabellifera" (Cymothoidae) (cf. ERHARD 1998a: 12).

– Insertion openings of the pleopods I–II
  In *Stenasellus* and *Protelsonia* the male pleopods I and II are inserted close together (figs. 1, 4, 8). The pleopod I is positioned at the back margin of pleonite I while pleopod II is located at the front margin of pleonite II. Presumably, the function of the male pleopods I as protective opercula for the pleopods II (cf. WILSON 1987, ERHARD 2001) might be responsible for their conspicuous approachment. The peculiar position of the insertion openings of the pleopods I and II has to be assumed as an apomorphous character state in respect to the tanaidacean, isopodan, phreatoicidean and oniscidean groundpatterns wherein the pleopods I and II are not approached conspicuously (cf. ERHARD 1995, 1996, 1997, 1998a). Presumably, the apomorphous character state of *Stenasellus* is present in the asellotan groundpattern as well. A close arrangement of the pleopods I and II occurs also in asellotan species with shortened pleonites I and II e.g. in *Asellus, Vermectias* and *Stenetrium* (figs. 5, 9; JUST & POORE 1992: fig. 5A; SEROV & WILSON 1995: fig. 15). This situation of shortened and, in the case of *Asellus* and

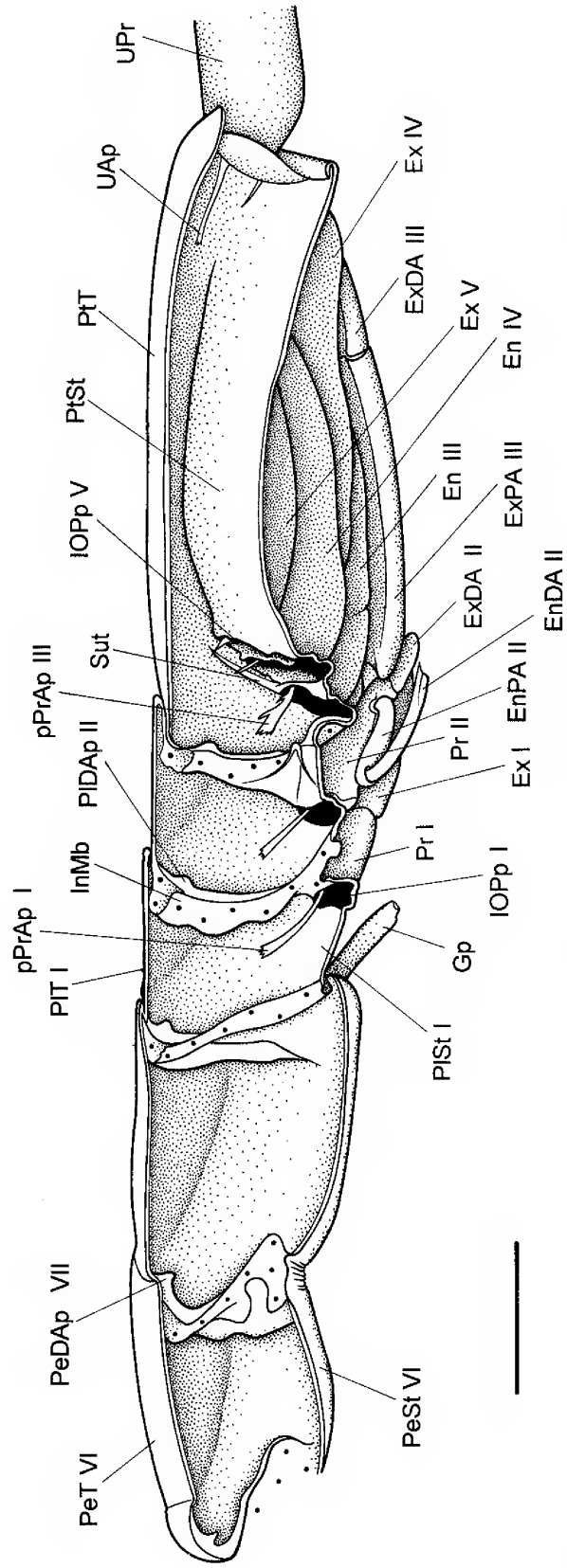

Fig. 8. *Stenasellus costai*, ♂, median longitudinal section through the skeleton of the pleon and the caudal pereion in medial view. – Scale: 1 mm.

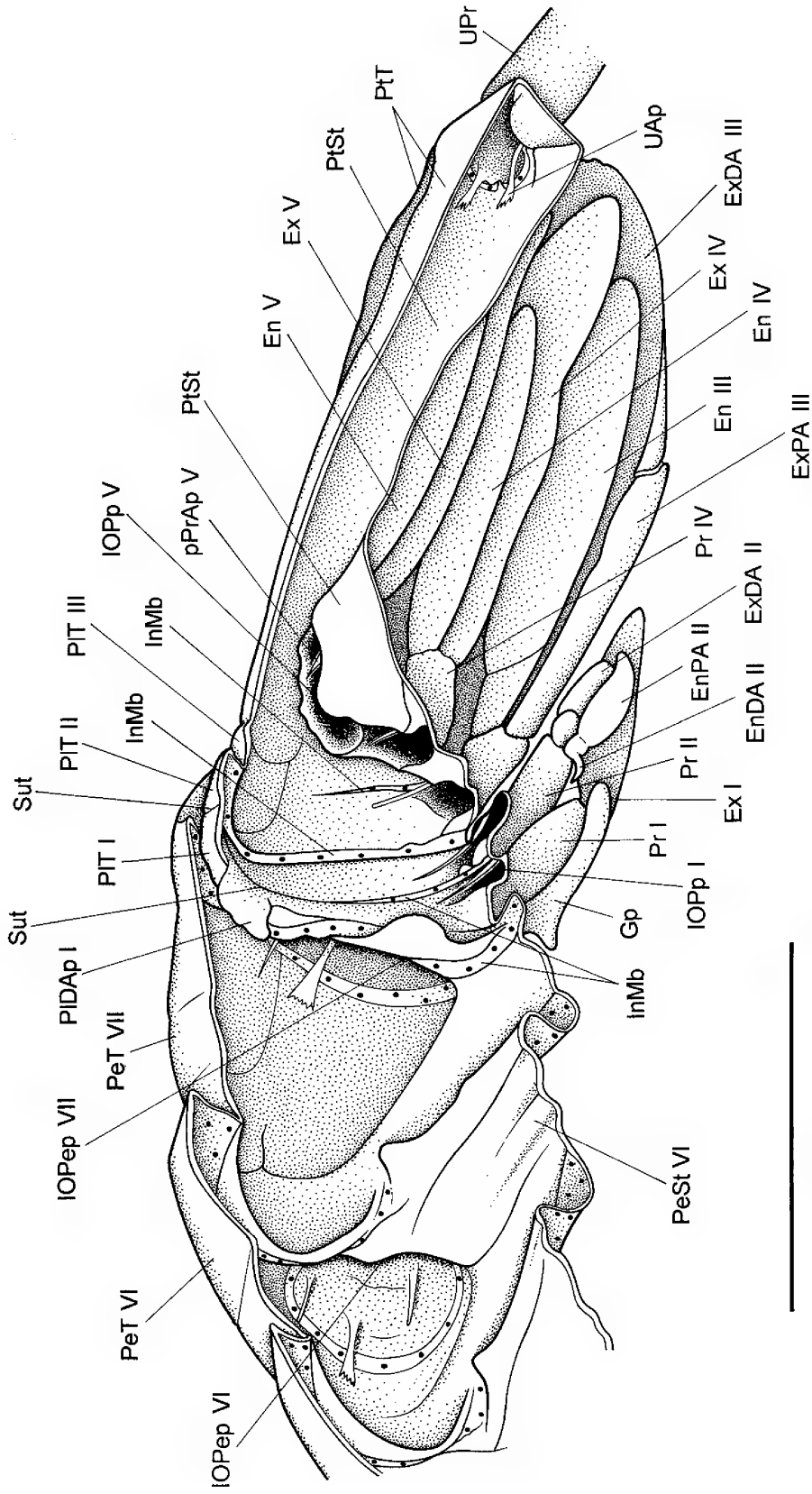

Fig. 9. *Asellus aquaticus*, ♂, median longitudinal section through the skeleton of the pleon and the caudal pereion in medial view. – Scale: 1 mm.

numerous further asellotan species, dorsally fused pleonites I and II could have been evolved from a *Stenasellus*-like precondition by the reduction of the anterior part of pleon segment I and the posterior part of pleon segment II.

– Insertion openings of the pleopods III–V
  Possibly as a result of the fusion of the pleonites IV–VI and the formation of a pleopodal chamber which is ventrally covered by the pleopod exopodites III, the insertion openings of the pleopods III–V are conspicuously approached in the investigated asellotan species (figs. 8–9).
  Presumably, this feature might represent an autapomorphous groundpattern character of the Asellota. In the tanaidacean, isopodan, phreatoicidean and oniscidean groundpatterns the pleopodal insertion openings III–V are clearly separated.

4.2. Musculature

The anatomical description of the musculature within the asellotan pleon trunk is mainly based on the species *Asellus aquaticus* (Asellidae). The documentation is supplemented by data gathered from *Protelsonia gjorgjevici* and *Stenasellus costai* (Stenasellidae).

4.2.1. Longitudinal musculature

According to ERHARD (1998a: 16) the dorsal and ventral longitudinal muscles (dLM, vLM) of the malacostracan pleon are differentiated into an external and an internal layer. Occasionally, a third central layer of the ventral muscle system may occur as it is the case in the Isopoda.

In the Phreatoicidea (cf. ERHARD 1998a) the longitudinal muscles are strongly and completely developed in comparison with the homologous musculature of the Oniscidea which shows some reductions of the ventral longitudinal muscles (cf. ERHARD 1995, 1996, 1997, 1998a). However, in the Asellota the longitudinal musculature appears to be even more reduced than in the Oniscidea, not least because of the fusion of the caudal pleon segments.

4.2.1.1. Dorsal longitudinal musculature (dLM) (figs. 10–12)

On contraction, the dorsal longitudinal muscles approximate the pleon tergites and work as extensors of the pleon and the large asellotan pleotelson.

4.2.1.1.1. Asellotan species

In the Phreatoicidea (ERHARD 1998a: 16) as well as in the Oniscidea (ERHARD 1995: 33) the pleonal internal layer of the dorsal longitudinal musculature actually is running at the inside of the external dorsal longitudinal muscles. In contrast, in *Asellus aquaticus* and in *Protelsonia gjorgjevici* the external layer is situated dorsally and dorsomedially to the internal layer and is therefore partly visible in medial view (fig. 10).

4.2.1.1.1.1. External layer

Mm 42–46: The external layer of the dorsal longitudinal musculature within the pleon of *Asellus aquaticus* (fig. 11) and *Protelsonia gjorgjevici* consists only of two segmental parts per body side. They are stretched between the front margins of the pleon tergites I and II (M 42) as well as between the pleon tergites II and III (M 43). In contrast to the stenasellid *Protelsonia,* the pleon tergites I and II are shortened and fused in *Asellus aquaticus* and only a slight internal suture has been retained (cf. chapt. 4.1.1.1., fig. 9). Nevertheless, some branches of the muscles Mm 42 and 43 have still preserved their segmental character and are attached at that suture though the pleon tergites I and II are no longer movable towards each other. However, other (lower) branches of Mm 42 and 43 are running transgressionally between the front margins of the pleon tergites I and III (fig. 11).

In the investigated asellotan species the muscles M 42 and M 43 each consist at one body side of three or four bundles as it is also the case in the serially homologous muscles of the pereion tergites. However, the serially homologous muscles of the pleon segments III–V, Mm 44–46, which are present within the groundpatterns of the Phreatoicidea and Oniscidea (ERHARD 1995, 1998a), are missing in *Asellus, Protelsonia* and *Stenasellus* (fig. 11).

The segmental dorsal longitudinal muscles of the Asellota (Mm 42–43) have to be considered homologous to the "Musculi dorsales segmentales" of some oniscidean species described by GRUNER (1953: 154) and to Mm 42–43 of the Oniscidea and the Phreatoicidea in ERHARD (1995: 33 and 1998a: 16).

4.2.1.1.1.2. Internal layer

M 41: The internal layer of the dorsal longitudinal musculature (dLM) within the pleon of *Asellus aquaticus* consists of segmental and transgressional elements (figs. 10, 12) as it is also the case in the Phreatoicidea and Oniscidea (cf. ERHARD 1998a: figs. 6–7). Probably on account of the formation of the large asellotan pleotelson the internal layer of the dLM in *Asellus* is ending at the front margin of the pleon tergite III while in the Phreatoicidea and Oniscidea M 41 is running back to the front margin of the pleonite VI (pleotelson).

As it is the case in the Phreatoicidea and the Oniscidea the internal layer of the dLM in *Asellus aquaticus* is composed within the pleonites I and II of four distinct and neighbouring bundles (fig. 10). Concerning the pass of these bundles the presumptive plesiomorphous status is retained in all units of the internal layer of the Phreatoicidea and Oniscidea (ERHARD 1998a: figs. 6–7) as well as in one bundle of the investigated asellotans (fig. 12: M41*): The typical muscle unit takes its origin on the front margin of the tergite of a trunk segment, passes transgressionally one segmental border without attachment on its way backwards and is inserted on the front margins of the following three tergites. Thus, one muscle unit runs through 4 segments. Each segment gives origin to one muscle unit (cf. ERHARD 1998a: 17).

In *Asellus aquaticus* only one muscle unit of M 41 shows roughly the above characterized typical pass (fig. 12: M 41*) while the other three units within the pleon are more or less abscured by special modifications as for example by the reduction of segmental parts and the fusion of muscle bundles. Also the muscle units of M 41 within the pereion are not completely congruent with the uniform arranged internal layer of the Phreatoicidea and Oniscidea (compare fig. 12 with ERHARD 1998a: figs. 6–7).

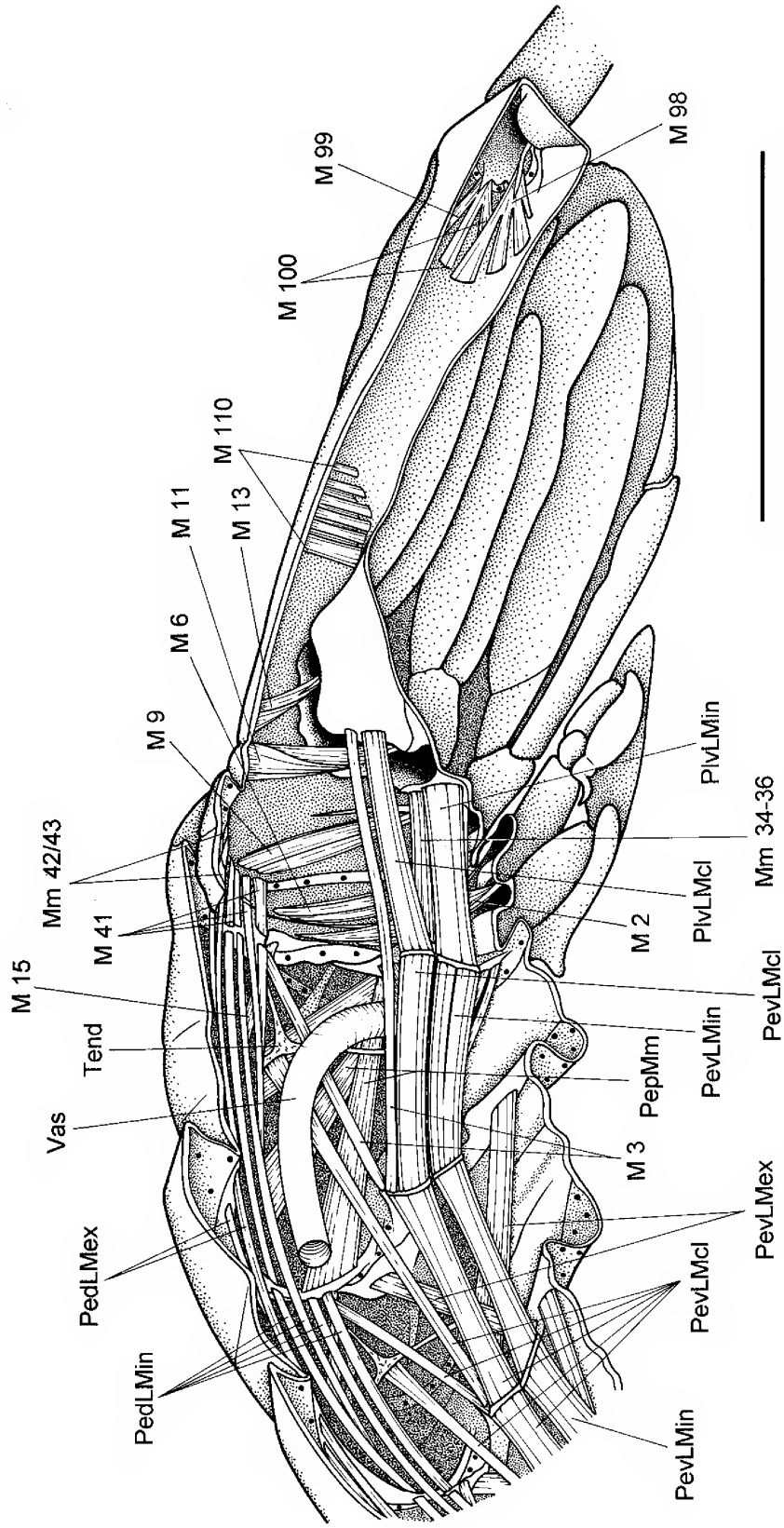

Fig. 10. *Asellus aquaticus*, ♂, median longitudinal section through the pleon and the caudal pereion in medial view showing the musculature and the vas deferens. Extrinsic locomotors of the pereiopod VI removed. – Scale: 1 mm.

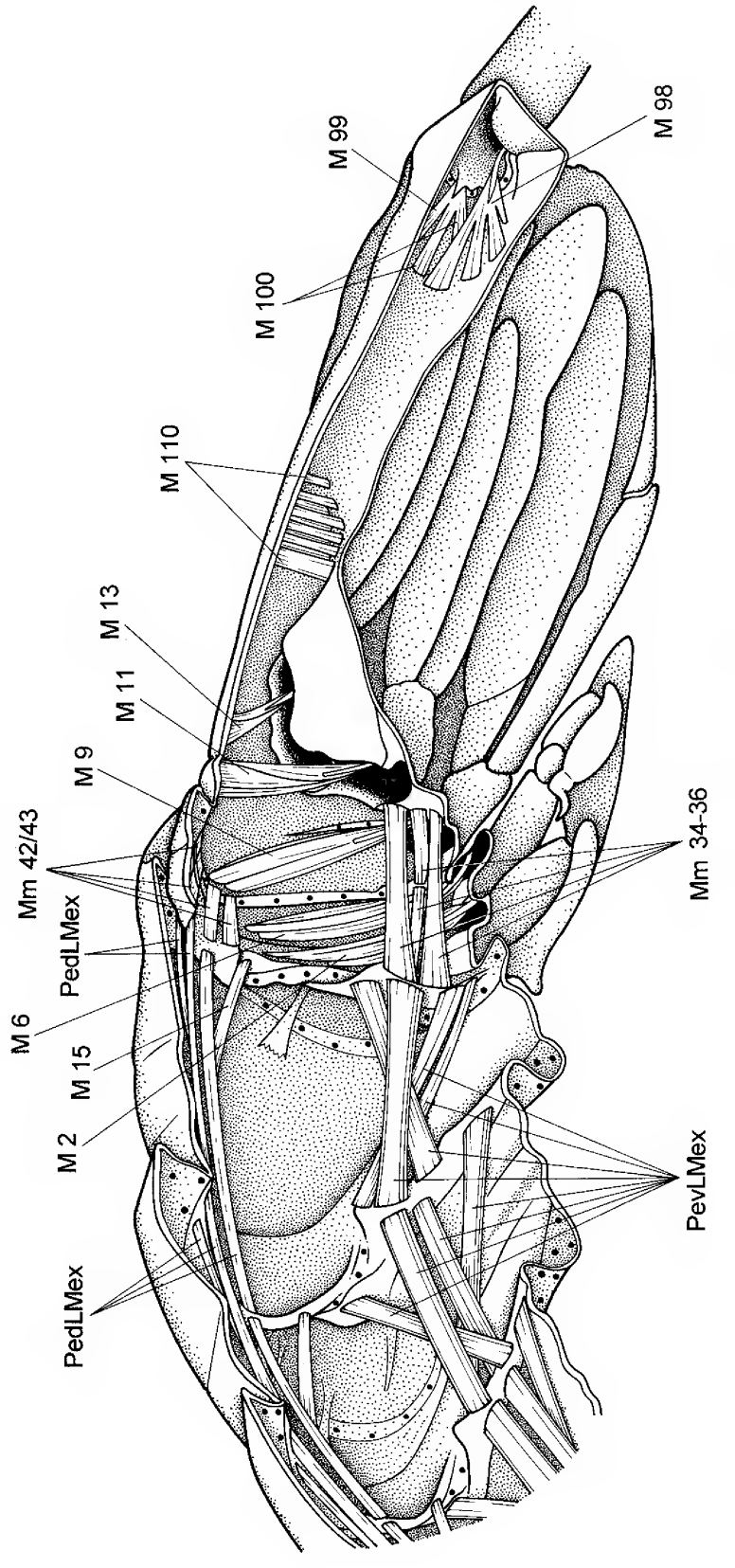

Fig. 11. *Asellus aquaticus*, ♂, median longitudinal section through the pleon and the caudal pereion in medial view showing the musculature. Internal layer of the dorsal longitudinal musculature, internal and central layers of the ventral longitudinal musculature and extrinsic locomotors of the pereiopods VI and VII removed. – Scale: 1 mm.

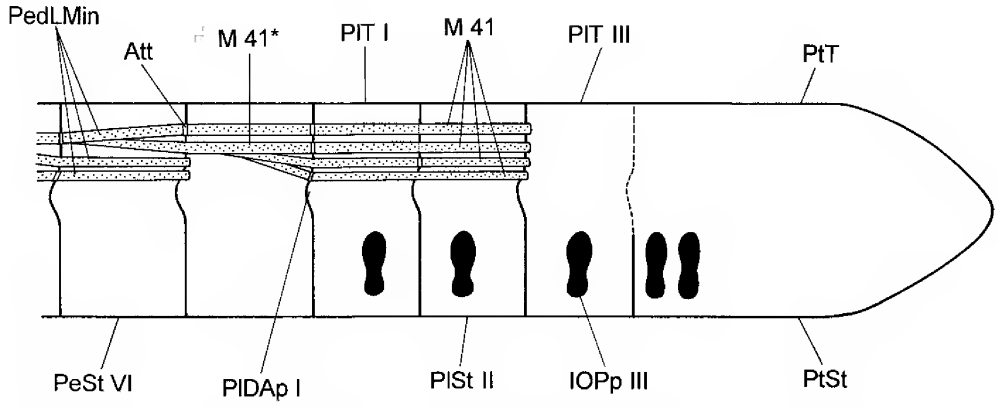

Fig. 12. Diagram of the internal layer of the dorsal longitudinal musculature (M 41) within the hypothetical groundpattern of the Asellota (compare with corresponding diagrams of the Phreatoicidea and Oniscidea in ERHARD 1998a: figs. 6–7).

The dorsal longitudinal muscle system M 41 of *Asellus aquaticus* has to be considered homologous to the "Musculi dorsales transgredientes" of some oniscidean species described by GRUNER (1953) and to M 41 of the Oniscidea and Phreatoicidea documented by ERHARD (1995: 33, 1998a: 17).

4.2.1.1.2. Comparison

– External layer (Mm 42–46)

Within the Phreatoicidea (ERHARD 1998a: 16) and the Oniscidea (ERHARD 1995: 33) the external layer of the pleonal dorsal longitudinal musculature consists of segmental muscles (Mm 42–46) which are stretched between the tergal front margins of the pleon segments I–VI. In *Asellus aquaticus* and *Protelsonia gjorgjevici* only two segmental units of the external layer within the pleonites I and II are still present while the muscles Mm 44–46 of the pleonites III–V are completely reduced (fig. 11). This reduction might be caused by the formation of the large asellotan pleotelson as well as the resulting immobility of the pleon tergites III–VI and the telson. Therefore, this apomorphous character state might also be present within the asellotan groundpattern. If a freely movable pleonite III actually might be existent in the groundpattern of the Asellota as reported by JUST & POORE (1992) in *Vermectias,* probably, M 44 within the pleonite III has additionally been retained within the asellotan groundpattern.

– Internal layer (M 41)

Within the groundpatterns of the Phreatoicidea, Oniscidea and presumably of the Isopoda the internal layer of the pleonal dorsal longitudinal musculature (M 41) is developed uniformly and is running through the entire pleon inserting on the front margin of pleonite VI (cf. ERHARD 1998a: figs. 6–7). In contrast, M 41 of *Asellus aquaticus* and *Protelsonia gjorgjevici* is already ending at the front margin of pleonite III (figs. 10, 12). This feature presumably is correlated with the formation of the large asellotan pleotelson by fusion of the caudal pleonites and the development of immovable segments. Following this, the apomorphous character state of *Asellus* and *Protelsonia* might also be present within the groundpattern of the Asellota because fused caudal pleonites occur in all asellotan species.

4.2.1.2. Ventral longitudinal musculature (vLM)

All ventral longitudinal muscles are flexors of the pleon. The ventral parts of the vLM approximate the pleonal sternites and thus shorten the ventral wall whereas the tergosternal subunits additionally lift the pleonal ventrum. As it is the status in the phreatoicidean and oniscidean groundpatterns (ERHARD 1998a: 19) the vLM of the Asellota is differentiated into an external, a central and an internal layer.

4.2.1.2.1. External layer (figs. 11, 13)

In the groundpattern of the asellotan trunk the external layer of the ventral longitudinal musculature (vLM) is composed of successive groups of segmental muscle units.

4.2.1.2.1.1. Asellotan species

Mm 34–36: The pleonal external layer of the vLM in *Protelsonia gjorgjevici* and *Asellus aquaticus* (fig. 11) extends from the back margin of the pereion sternite VII to the front margin of the pleon sternite IV which is incorporated into the large asellotan pleotelson. In the stenasellid *Protelsonia* as well as in the asellotan groundpattern the segmental character of the successive muscle groups Mm 34–36, which consist of about 3–4 branches respectively, still is retained (fig. 13). M 34 is stretched between the back margins of pereion sternite VII and pleon sternite I and M 35 extends between the back margins of the pleon sternites I and II. However, M 36 originates on the back margin of pleon sternite II but passes two segmental borders and is inserted not before the front margin of pleon sternite IV. The muscles Mm 34–36 of *Protelsonia* are homologous to Mm 34–36 of the Oniscidea (ERHARD 1995: 30) and the Phreatoicidea (ERHARD 1998a: 19) as well as to the "Musculi ventrales majores" described by GRUNER (1953).

In *Asellus aquaticus* the pleon segments I and II are shortened and dorsally fused with each other (cf. chapt. 4.1.1.). Presumably on account of this fact the segmental muscle units of the external layer are forming together few transgressional muscle bundles running without stopping from the back margin of pereion segment VII to the front margin of pleon segment IV. However, one or two branches are still inserting on the segmental border between pleon sternite II and III (fig. 11). The fusion of segmental units of the external layer of the vLM in *Asellus* has to be considered as an apomorphous character state in respect to the asellotan groundpattern. In contrast, within the pereion of *Asellus* the muscle branches of the external layer are still segmental units. They are crossing each other in a conspicuous manner (fig. 11) while in *Protelsonia* the branches of the external layer are running parallel in the pereion as well as in the pleon.

Mm 37–39: In the Asellota the muscles of the external layer of the vLM in the fused pleonites IV–VI (asellotan pleotelson) are missing while corresponding muscles occur in the caudal pleonites of the Oniscidea and Phreatoicidea (cf. ERHARD 1995: 30, 1998a: 19)[4].

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[4] In the Oniscidea all pleonal muscles of the external longitudinal musculature Mm 34–39 are present while in the Phreatoicidea only Mm 34–38 occur and M 39 is lacking (ERHARD 1995, 1998a).

4.2.1.1.1.2. Comparison

– Caudal muscles of the pleonal external layer of the vLM

As it is also the case with the internal and central layers of the vLM, the pleonal external layer of the Asellota is shortened on account of the formation of the large asellotan pleotelson and the occurrence of immovable caudal pleon segments. The complete reduction of the muscles Mm 37–39 represents an apomorphous character state of the Asellota in respect to the groundpatterns of the Isopoda, Oniscidea and Phreatoicidea (cf. ERHARD 1998a: 19).

4.2.1.2.2. Central layer (figs. 10, 14)

4.2.1.2.2.1 Asellotan species

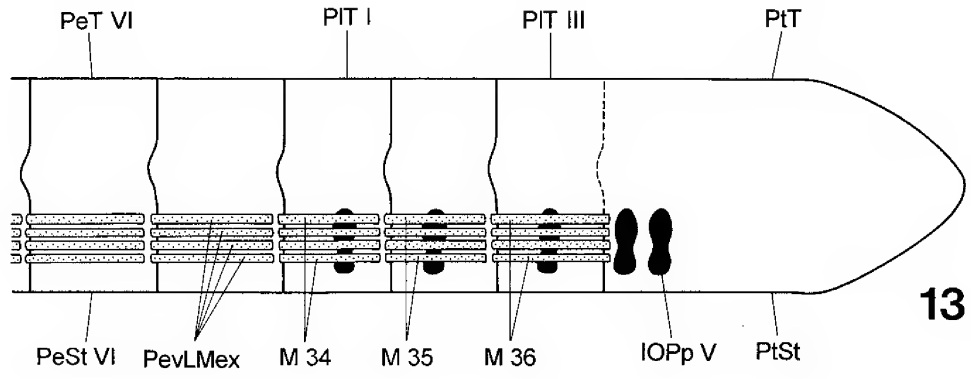
The central layer of the asellotan ventral longitudinal musculature (vLM) is composed of tergosternal as well as ventral parts.

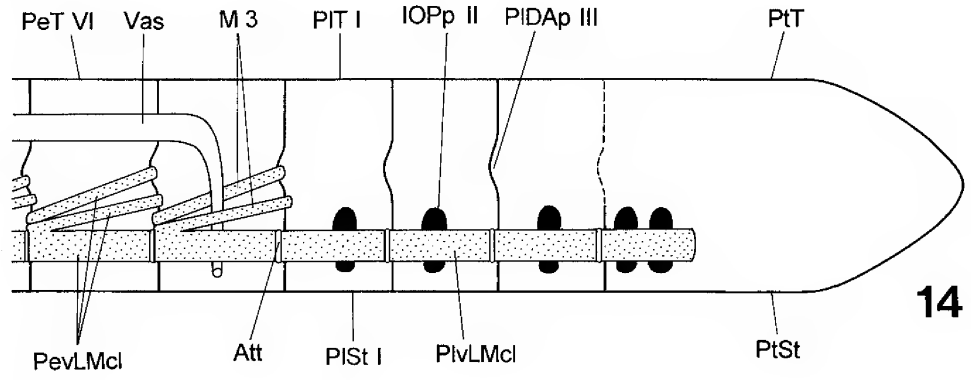
The tergosternal muscle units, which are represented by segmental muscle pairs, take their origin on the "dorsal apophyses" of the pleonal and pereional tergites as it could be shown in *Protelsonia* and *Stenasellus* (fig. 14). In *Asellus aquaticus* the origin of the lower branch of the tergosternal pair within each pereion segment is not located at the tergal front margin but has been shifted backwards to the caudal half of the tergite where the muscle is attached at a tendon of connecting tissue (fig. 10). This situation might be an apomorphous conditions of *Asellus* while the status present in *Protelsonia* and *Stenasellus* corresponds clearly with the situation in the groundpattern of the Phreatoicidea and Oniscidea (cf. ERHARD 1998a: figs. 9–10). Herein all tergosternal muscle units of the central layer take their origin on the tergal front margins.

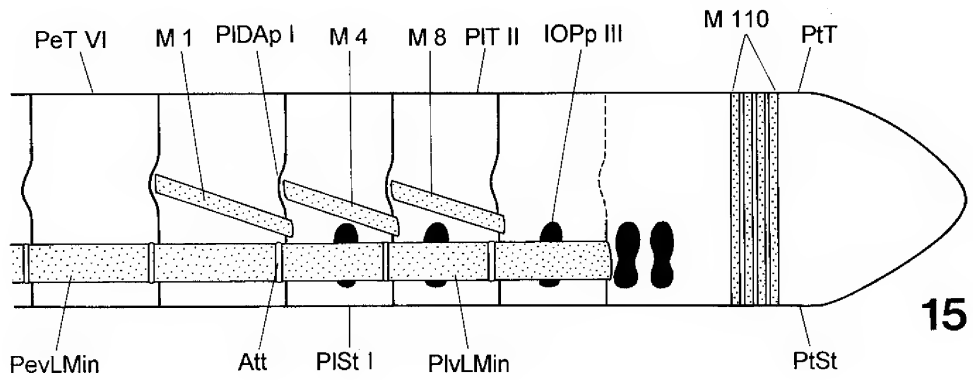
Originating on the tergal front margin of a segment one tergosternal muscle pair of the central layer in the asellotan trunk descends in ventrocranial direction, passes two segmental borders and is attached on the back margin of the sternite within the pre-preceding segment (fig. 14). There, the tergosternal component gets in touch with the ventral longitudinal muscle string of the central layer. The individual branches of that string are condensed to a uniform strong muscle cord which does not allow to determine distinct muscle bundles. As it is the case in the Oniscidea, the ventral muscle cord of the central layer seems to be more or less isolated from the tergosternal parts.

In the investigated asellotan species the ventral string of the central layer is inserted on the back margins of all pereional sternites (figs. 10, 14). Behind the pereion sternite VII the ventral muscle cord of *Asellus aquaticus,* however, runs backwards transgressionally without attachment on the segmental borders of the pleon (fig. 10). This feature might be apomorphous in relation to the asellotan groundpattern while in *Stenasellus costai* the pleonal ventral muscle cord of the central layer is still attached on the back margins of the pleon sternites I–III (fig. 14). In *Asellus* as well as in *Stenasellus* the ventral string is caudally inserted on the pleotelsonic ventrum beyond the insertion openings of the pleopods IV and V (figs. 10, 14).

In *Protelsonia* the ventral string of the central layer is already ending at the front margin of pleon sternite I which might represent an apomorphous character state in respect to *Asellus, Stenasellus* and the asellotan groundpattern. In the Oniscidea and Phreatoicidea the corresponding ventral string is inserted at the back margins of all







Figs. 13–15. Diagrams of the ventral longitudinal musculature (vLM) within the hypothetical groundpattern of the Asellota (compare with corresponding diagrams of the Phreatoicidea and Oniscidea in ERHARD 1998a: figs. 9–12). – 13. External layer of the vLM (Mm 34–36); – 14. central layer of the vLM and pass of the vas deferens; – 15. internal layer of the vLM and pleotelsonic muscle M 110.

pleon sternites and is ending at the front margin of pleon segment VI (pleotelson) (cf. ERHARD 1998a: figs. 9–10).

In the investigated asellotan species the tergosternal muscle units of the central layer are represented within the pereion segments by two bundles per body side. The most caudal pair of these tergosternal pereional subunits, M 3, is still retained in the Asellota. However the caudal pleonal homologa, Mm 7 and 105–108, present for example in the phreatoicidean groundpattern (ERHARD 1998a: 19), are completely reduced within the pleon of the investigated asellotan species (figs. 10, 14).

M 3: The tergosternal component of the central layer muscle M 3 arises in *Protelsonia gjorgjevici* and *Stenasellus costai* with two bundles on the lateral front margin ("dorsal apophysis") of the pleon tergite I, passes cranioventrally and is inserted on the back margin of the pereion sternite VI (fig. 14). There it gets in touch with the ventral cord of the central layer of the vLM. A distinct ventral branch of M 3 could not be determined. Presumably, it fused with other ventral bundles to the uniform ventral string of the central layer. Between both tergosternal parts of M 3 the vas deferens of one body side is descending towards the male genital papilla.

In *Asellus aquaticus* a corresponding condition of M 3 occurs, however, the lower tergosternal branch is shifted ventrally which causes a conspicuous approachment to the ventral cord of the central layer (fig. 10). Furthermore, beyond the front margin of pleon segment I, the muscle is lengthened in caudal direction and is ending within the pleotelson nearby the insertion of the ventral cord of the central layer. Both features of *Asellus* might be apomorphous conditions differing from the status of *Protelsonia* and *Stenasellus* which shows an identical character state of the lower tergosternal M 3 branch with those present in the Oniscidea and Phreatoicidea (cf. ERHARD 1998a: figs. 9–10).

The asellotan muscle M 3 has to be considered homologous to M 3 of the Oniscidea (ERHARD 1995, 1996, 1997) and the Phreatoicidea (ERHARD 1998a) as well as to the corresponding branch of the "Musculi dorsoventrales procurrentes" described by GRUNER (1953).

Mm 7, 105–108: The tergosternal subunits of the central layer muscles Mm 7 and 105–108 within the pleonites II–V (= serial homologa to M 3) are present within the groundpattern of the Phreatoicidea (cf. ERHARD 1998a: 21) but could not be shown in the investigated asellotan species. It has to be assumed, however, that the ventral longitudinal parts of the muscles in the Asellota have been retained in the shape of the condensed ventral cord of the pleonal central layer of the vLM.

M 40: In the Phreatoicidea and the Oniscidea the muscle M 40 represents the most caudal part of the ventral cord of the pleonal central layer stretched between the back margin of pleon sternite IV and the pleotelsonic front margin (cf. ERHARD 1998a: figs. 9–10). Even in the Phreatoicidea, which show a very complete and primitive type of the ventral longitudinal musculature, M 40 lacks any tergosternal muscle unit. It solely serves to attach the central layer cord at the pleotelsonic sternite.

In the Asellota M 40 is either completey reduced or incorporated within the ventral cord of the central layer and might then represent the most caudal part of that cord. However, most attachment points of the ventral string at the caudal pleonal ventrum are reduced in the Asellota wherefore a clear demarcation of M 40 is impossible.

4.2.1.2.2.2. Comparison

– Ventral cord of the central layer of the vLM

In the groundpattern of the isopodan trunk the segmental muscle units of the central layer of the vLM are composed of tergosternal parts which are originating on the tergal front margins and which are descending in cranioventral direction. They have ventral prolongations forming together a ventral muscle cord. In the Phreatoicidea the formation of this ventral cord by distinct descending subunits is still clearly visible and is described in detail by ERHARD (1998a: 19, figs. 8–9).
In contrast, the homologous ventral muscle cord of the central layer in the Asellota and the Oniscidea is only represented by a uniform condensed string and separate bundles are no longer distinguishable (fig. 14; ERHARD 1998a: 10). Furthermore, the shared identity of tergosternal and ventral parts is very inconspicuously, because these muscles are separated to a great extent. The condensation of the segmental subunits of the central layer forming a uniform and separated ventral muscle cord has to be considered as an apomorphous feature of the Asellota and Oniscidea in respect to the isopodan groundpattern which includes a phreatoicidean-like condition.

– Tergosternal branches of the central layer of the vLM

In the Phreatoicidea the pereionite VII and the pleonites I–V are equipped with paired tergosternal branches of the central layer of the ventral longitudinal musculature Mm 3, 7, 105–108 (ERHARD 1998a: fig. 9). Also all pleonites of the presumptive isopodan sistergroup Tanaidacea (*Apseudes latreillii*) are showing tergosternal branches of the central layer of the vLM.
In contrast, the homologous muscles within the pleon segments II–V, Mm 105–108, are completely reduced in the Oniscidea and the Asellota (fig. 14; ERHARD 1998a: fig. 10). While in the Oniscidea one branch of the tergosternal part of M 7 within the pleonite I is still retained, this muscle is also missing in the investigated asellotan species. However, the serial homologon to Mm 7 and 105–108 within the pereionite VII, M 3, and those serial homologa within the other pereionites are developed as muscle pairs in the Oniscidea and Asellota as well as in the Phreatoicidea. The complete reduction of the tergosternal branches of the muscles Mm 105–108 in the Oniscidea and Asellota as well as the lack of the tergosternal branches of M 7 in the Asellota might represent apomorphous character states in respect to the isopodan groundpattern.

– Position of the vasa deferentia

At least in the groundpatterns of the Oniscidea (ERHARD 1995a: 29, 1998a: fig. 10) and the Asellota (fig. 14) as well as in the valviferan *Saduria entomon* the vas deferens of one body side in male specimens passes between the two tergosternal branches of M 3. In contrast, within the phreatoicidean groundpattern the vas deferens runs lateral to the tergosternal part of M 3 (ERHARD 1998a: fig. 9) as it is also the condition in male specimens of the tanaidacean *Apseudes latreillii.* As already discussed by ERHARD (1998a: 24) the plesiomorphous character state in respect to the isopodan groundpattern might represent the phreatoicidean condition. The location of the vas deferens between the M 3 branches in the Oniscidea, Asellota, Valvifera and, presumably, the flabelliferan groups *Aega* and *Sero-*

lis (cf. JUST & POORE 1992) might probably correspond to the medial migration of the male genital papillae off the pereiopod coxopodites VII.

4.2.1.2.3. Internal layer (figs. 10, 15)

The internal layer of the pleonal ventral longitudinal musculature in the groundpattern of the Isopoda is composed of segmental tergosternal subunits which have ventral continuations forming together a strong ventral muscle cord. The muscle subunits of the internal layer take their origin at the "dorsal apophyses" of the tergites, descend ventrocaudally, passing three segmental borders, and are inserted on the ventrum of the corresponding segment. This plesiomorphous arrangement of the internal layer of the vLM is nowadays still retained within the taxon Phreatoicidea and is described by ERHARD (1998a: 25, fig. 11). The basic plan of the internal layer within the asellotan trunk (fig. 15) is more or less obscured by special modifications described below.

4.2.1.2.3.1. Asellotan species

The tergosternal branches of the internal layer of the vLM are completely reduced in most trunk segments of the investigated asellotan species: In *Asellus aquaticus* the tergosternal branches of all segments are missing (fig. 10) while in the stenasellids *Protelsonia gjorgjevici* and *Stenasellus costai* the dorsoventral muscle units Mm 1, 4, and 8 of the internal layer within the pereionite VII and the pleonites I–II are still retained (fig. 15). In contrast to the basic phreatoicidean pattern the tergosternal branches of *Protelsonia* and *Stenasellus* have lost their connections with the ventral cord of the internal layer as it occurs also in subordinate taxa of the Oniscidea (Synocheta, Crinocheta; cf. ERHARD 1995, 1997). Thus, the ventral cord appears to be an isolated structure within the asellotan species and a relation between tergosternal and ventral components of the internal layer of the vLM is not obvious. Only the comparison with the condition of the Phreatoicidea and, to a limited extent, of the Oniscidea can explain the origin and the shared identity of tergosternal and ventral muscle units (cf. ERHARD 1998a: figs. 11–12).

The ventral cord of the internal layer of the vLM in the investigated asellotans *Asellus, Protelsonia* and *Stenasellus* is formed by different subunits which, however, appear very condensed. Therefore, the ventral cord has the shape of a uniform muscle string and the identification of distinct segmental components is rather difficult. This ventral muscle string is attached on the back margins of all pereion sternites (figs. 10, 15) and is ending on the front margin of pleon sternite IV (asellotan pleotelson). In *Protelsonia gjorgjevici* and *Stenasellus costai* further points of insertion within the pleon are the back margins of the pleonal sternites I and II (fig. 15). However, in *Asellus aquaticus* the ventral muscle cord is running transgressionally between the back margin of pereion sternite VII and the caudal end at the front margin of pleon sternite IV without further points of attachment (fig. 10). The latter condition might be an apomorphous status in respect to the asellotan groundpattern.

While the different parts of the asellotan ventral cord of the internal layer cannot be homologized with corresponding subunits of the Phreatoicidea and Oniscidea for the above mentioned reason, the retained tergosternal components of *Protelsonia gjorgjevici* and *Stenasellus costai* are clearly identifiable with homologa of other isopodan taxa due to their spatial position (fig. 15):

M 1: Arises on the "dorsal apophysis" of pereion tergite VII and is inserted on the front margin of pleon sternite I. Homologous to M 1 of the Oniscidea (ERHARD 1995: 15) and the Phreatoicidea (ERHARD 1998a: 25).

M 4: Arises on the "dorsal apophysis" of pleon tergite I and is inserted on the front margin of pleon sternite II. Homologous to M 4 of the Oniscidea (ERHARD 1995: 15) and the Phreatoicidea (ERHARD 1998a: 25).

M 8: Arises on the "dorsal apophysis" of pleon tergite II and is inserted on the front margin of pleon sternite III. Homologous to M 8 of the Oniscidea (ERHARD 1995: 17) and the Phreatoicidea (ERHARD 1998a: 25).

Mm 104, 10, 12, 14: The tergosternal components of the internal layer M 104 (pereionite VI) and Mm 10, 12, 14 (pleonites III, IV, V) described in the taxa Oniscidea and Phreatoicidea (ERHARD 1998a: figs. 11–12) could not be shown in the investigated asellotan species. However, the ventral components of these muscles presumably might be incorporated into the ventral cord of the internal layer of the vLM.

4.2.1.2.3.2. Comparison

– Tergosternal components of the internal layer

  In the groundpatterns of the Phreatoicidea and Oniscidea tergosternal components of the internal layer of the ventral longitudinal musculature (vLM) are present in all pereion and pleon segments (ERHARD 1998a: figs. 11–12). In the investigated asellotan species only within the pereionite VII and the pleonites I and II tergosternal muscle units could be shown (Mm 1, 4, 8; fig. 15). If this pattern can be confirmed also for non-aselloidean Asellota the reduction of tergosternal muscle units of the internal layer in the pereion segments I–VI and in the caudal pleon segments III–V (Mm 10, 12, 14) might represent an apomorphous character state of the Asellota in respect to the isopodan groundpattern.

– Separation of tergosternal and ventral parts of the internal layer

  Within the groundpattern of the Isopoda as well as in the Phreatoicidea the tergosternal parts of the muscle units of the internal layer of the vLM (e.g. Mm 104, 1, 4, 8, 10, 12, 14; cf. ERHARD 1998a: fig. 11) are directly connected with their ventral prolongations which are forming a ventral muscle cord. If tergosternal subunits have been retained in the Asellota (e.g. Mm 1, 4, 8 in *Protelsonia* and *Stenasellus),* they are completely separated from the ventral cord of the internal layer which represents an apomorphous condition (fig. 15). In the investigated oniscidean species the tergosternal subunits of the pereion and the cranial pleon segments still are connected with their ventral continuations but the caudal muscles Mm 10, 12, and 14 show also separated tergosternal and ventral parts (cf. ERHARD 1998a: fig. 12).

– Pass of the tergosternal parts of the internal layer

  In the groundpatterns of the Phreatoicidea and presumably of the Isopoda the tergosternal parts of the pereional and pleonal segmental subunits of the internal layer of the vLM are originating at the tergal front margins (dorsal apophyses), pass one segmental border without attachment on its way backwards and are inserted together with the ventral parts of the internal layer on the back margin of the next following sternite by a tendon of connective tissue (cf. ERHARD 1998a:

fig. 11). An equivalent pattern is also present in the pereion segments of the Oniscidea, for example in *Ligia oceanica* (cf. ERHARD 1998a: fig. 12). This conformity with the phreatoicidean type of insertion indicates that this pattern might be a primitive condition. However, in the oniscidean species the tergosternal parts of the pleonal muscles Mm 1, 4, 8, 10, 12, 14 are running backwards through the segment of their origin and insert on the following segmental border at which also the ventral cord is attached (cf. ERHARD 1998a: fig. 12). Thus, the type of insertion within the oniscidean pleon is different from the oniscidean pereion and all phreatoicidean trunk segments because the point of attachment of the tergosternal muscle units at the back margin of a pleonite has been shifted forwards to the preceding segmental border. This presumptive apomorphous character state applies also to the retained tergosternal subunits within the pereionite VII and the pleonites I and II in the Asellota (fig. 15). In these segments the tergosternal muscles Mm 1, 4, and 8 insert at the segmental borders (front margins of pleonites) as it is also the case in the Oniscidea.

– Condensation of the ventral cord of the internal layer
  In the groundpatterns of the Phreatoicidea and presumably of the Isopoda the ventral parts of the pleonal muscle units Mm 104, 1, 4, 8, 10, 12, 14 of the internal layer of the vLM are still distinct muscle bundles forming together the ventral cord (cf. ERHARD 1998a: figs. 5, 11). In contrast, in the Oniscidea as well as in the Asellota the pleonal muscle units of the ventral cord are condensed and are forming a uniform string. Only a higher microscopical magnification of the ventral cord can show the compound structure (figs. 10, 15; ERHARD 1998a; figs. 12). This feature might represent apomorphous character states of the Oniscidea and Asellota in respect to the isopodan and phreatoicidean groundpatterns.

– Caudal insertion of the ventral cord of the internal layer
  Within the groundpatterns of the Phreatoicidea, Oniscidea and presumably of the Isopoda the ventral cord of the internal layer of the pleonal ventral longitudinal musculature is running through the entire pleon and inserts on the front margin of pleon sternite VI (cf. ERHARD 1998a; figs. 11–12). In contrast, the ventral internal cord of the investigated asellotan species is already ending at the front margin of pleon sternite IV (figs. 10, 15). This feature presumably is correlated with the formation of the large asellotan pleotelson by fusion of the caudal pleonites and the development of immovable segments. Following this, the apomorphous character state of a shortened ventral cord might be present within the groundpattern of the Asellota because fused caudal pleonites occur in all asellotan species.

4.2.2. Stabilizers of the pleonal "dorsal apophyses" (figs. 11, 16–18)

4.2.2.1 Asellotan species

4.2.2.1.1. Mm 18–26a

In the Phreatoicidea and the Oniscidea the neighbouring lateral front margins of the pleon tergites ("dorsal apophyses") are braced by the horizontal muscles Mm

18–26a which might be derivates of the dorsal longitudinal musculature (figs. 16–17; ERHARD 1995, 1996, 1997, 1998a). Corresponding muscles could not be shown within the pleon of *Asellus aquaticus* (figs. 10–11). However, in the stenasellids *Protelsonia gjorgjevici* and *Stenasellus costai,* which have still well developed pleonites I and II, Mm 18/19 and Mm 20/21 are retained (fig. 18):

Mm 18/19: Composed of a uniform broad muscle bundle. Arises on the front margin of pleon tergite I and is inserted on the front margin of pleon tergite II. Homologous to Mm 18/19 of the Phreatoicidea (ERHARD 1998a) and the Oniscidea (ERHARD 1995, 1996, 1997).

Mm 20/21: Composed of a uniform broad muscle bundle. Arises on the front margin of pleon tergite II and is inserted on the front margin of pleon tergite III. Homologous to Mm 20/21 of the Phreatoicidea (ERHARD 1998a) and the Oniscidea (ERHARD 1995, 1996, 1997).

Mm 22–26a: The serially homologous muscles to Mm 18/19 and 20/21 are completely reduced within the fused pleonites III–V of the investigated asellotan species. Mm 22–26a are present in the Phreatoicidea (ERHARD 1998a) and the Oniscidea (ERHARD 1995, 1996, 1997).

4.2.2.1.2. Mm 15–17

Within the phreatoicidean and oniscidean pereion there are serial homologa to the pleonal muscles Mm 18–26a (figs. 16–17; ERHARD 1995, 1996, 1997, 1998a). Corresponding muscles could also be shown within the pereion of *Asellus, Stenasellus* and *Protelsonia* (figs. 11, 18). The pass of these branches is exactly in accordance with the run of the corresponding muscles in the oniscideans *Ligia oceanica, Mesonicus alpicola, Oniscus asellus* and *Actaecia bipleura.* M 15 within the pereion segment VII of the investigated asellotan species is described in detail:

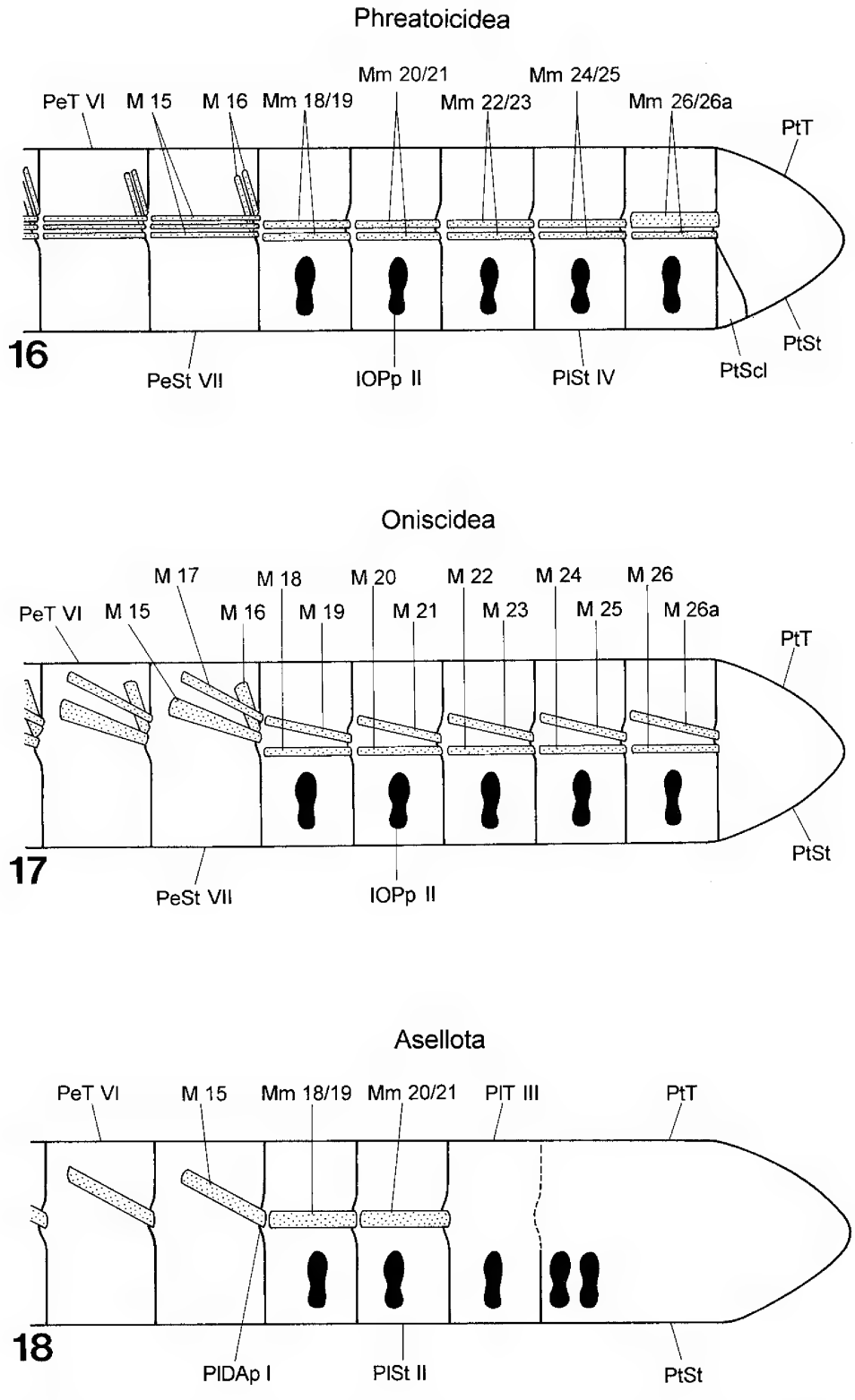
M 15: Arises at the mid-region of the pereion tergite VII and is inserted on the front margin ("dorsal apophysis") of pleon tergite I. Composed of one bundle. Homologous to M 15 of the Phreatoicidea and Oniscidea (cf. ERHARD 1995, 1996, 1997, 1998a).

Mm 16, 17: Both tergal stabilizers, which are stretched between pereionite VII and pleonite I, occur within the oniscidean groundpattern (fig. 17; cf. ERHARD 1995, 1996, 1997). In the Phreatoicidea only M 16 could be shown with certainty (fig. 16; cf. ERHARD 1998a) while in the investigated asellotan species Mm 16 and 17 are completely missing (fig. 18).

4.2.2.2. Comparison

– Reduction of Mm 22–26a

  Within the groundpatterns of the Phreatoicidea and Oniscidea the pleon segments I–V are equipped with the tergite locomotors Mm 18–26a (figs. 16–17). Presumably, the lack of the tergite stabilizers and locomotors Mm 22–26a in asellotan species is correlated with the fusion of the caudal pleonites and the formation of immovable pleon segments in the Asellota (fig. 18). Therefore, the reduction of caudal pleonal stabilizers might be an apomorphous character state of the group. However, in the asellotan *Vermectias,* which has retained a freely movable



Figs. 16–18. Diagrams of the stabilizers and locomotors of the tergal "dorsal apophyses" (Mm 15–26a) within the isopodan pleon. – 16. Groundpattern Phreatoicidea; – 17. groundpattern Oniscidea; – 18. groundpattern Asellota.

pleonite III, also Mm 22/23 within the pleonite III, probably, might still be existent.

– M 15

In the Phreatoicidea M 15 is running between the "dorsal apophyses" of the tergite front margins of pereionite VII and pleonite I and passes from cranial to caudal (fig. 16; ERHARD 1998a: fig. 8). This pass might characterize a plesiomorphous pattern and corresponds to the pass of all serial homologa in other trunk segments of the Phreatoicidea as well as to the pass of the pleonal serial homologa of the Oniscidea and the Asellota (figs. 17–18).
In the groundpattern of the Oniscidea (fig. 17; ERHARD 1997: fig. 27) and in the investigated asellotan species (fig. 18) M 15 arises at the mid-region of pereion tergite VII, passes ventrocaudally and is inserted on the "dorsal apophysis" of the pleon tergite I. The serial homologa to M 15 within the pereionites I–VI are passing in a corresponding way. It is assumed that these special ventrally directed passes of M 15 and its pereional serial homologa represent derived character states of the Oniscidea and Asellota.

– M 16

In contrast to the pleonal situation, the pereion segments of the Phreatoicidea and Oniscidea have additional stabilizers and locomotors of the tergite front margins (figs. 16–17). Within the pereion segment VII the muscle M 16 is present in the Phreatoicidea and Oniscidea. A corresponding muscle could not be shown so far in the Asellota (fig. 18) which presumably might be an apomorphous character state of the group[5]).

4.2.3. Extrinsic pleopod locomotors (figs. 11, 19)

4.2.3.1. Asellotan species

In the investigated asellotan species *Protelsonia gjorgjevici, Stenasellus costai* and *Asellus aquaticus* the pleon segments comprise dorsoventral muscles which are able to move the pleopods backwards (remotors). Because extrinsic dorsoventral promotors obviously are missing in the Asellota a forward directed movement of the pleopods is mainly caused by intrinsic pleopod promotors (cf. ERHARD 2001).

The pleopods in terrestrial isopods usually are tipped up to the pleon ventrum wherefore the promotors and remotors have been described by ERHARD (1995, 1996, 1997, 1998b) as pleopod "depressors" and "levators".

4.2.3.1.1. Pleopod promotors

Mm 111, 5, 112–114: The tergal promoters of the pleopods I–V, present in the phreatoicidean groundpattern (ERHARD 1998a: figs. 13–14), are completely missing in the investigated asellotan species (figs. 11, 19).

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[5]) A further muscle M 17 occurs only in oniscidean species within the pereionite VII but it presumably might be a derivate of M 15 on account of its spatial position (cf. ERHARD 1995, 1996, 1997, 1998a).

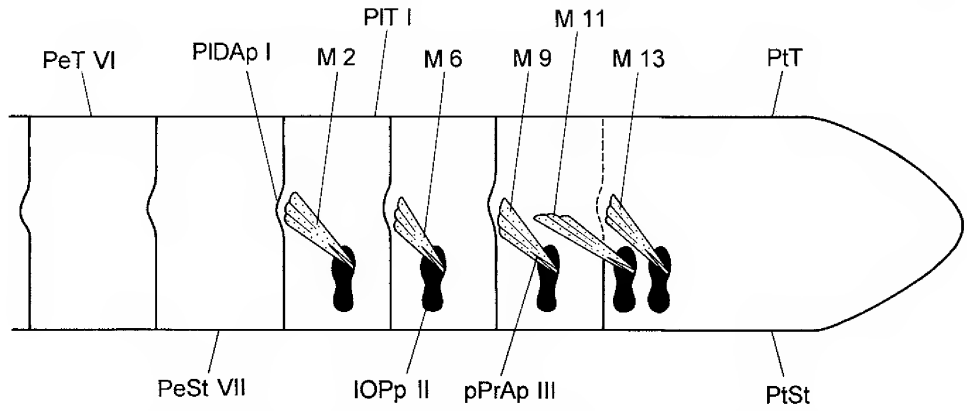


Fig. 19. Diagram of the extrinsic pleopodal locomotors (Mm 2, 6, 9, 11, 13) within the hypothetical groundpattern of the Asellota (compare with corresponding diagrams of the Phreatoicidea and Oniscidea in ERHARD 1998a: figs. 14–15).

4.2.3.1.2. Pleopod remotors

Each tergal pleopod remotor of the investigated asellotan species is composed of two or three bundles (figs. 11, 19). The asellotan remotors have to be considered homologous to the muscles Mm 2, 6, 9, 11, 13 of the Phreatoicidea (ERHARD 1998a) and Oniscidea (ERHARD 1995, 1996, 1997).

M 2: Arises on the front margin of the pleon tergite I and is inserted on the posterior apophysis of pleopod protopodite I.

M 6: In *Protelsonia* and *Stenasellus* the muscle arises on the front margin of pleon tergite II and is inserted on the posterior apophysis of pleopod protopodite II (fig. 19). In *Asellus* the pleonites I and II are shortened and their tergites have fused (chapt. 4.1.1.1.) wherefore M 6 arises immediately behind M 2 on the joint tergite of the pleon segments I and II (fig. 11). The latter arrangement of Mm 2 and 6 in *Asellus* has to be considered as an apomorphy in respect to the asellotan groundpattern and presumably occurs in all asellotan groups with shortened and fused pleonites I and II.

M 9: In all investigated asellotan species the muscle arises on the front margin of pleon tergite III and is inserted on the posterior apophysis of pleopod protopodite III.

M 11: Arises behind M 9 on the tergite of pleon segment III which is still demarcated by a suture from the large pleotelson (pleonites IV–VI + telson) in *Asellus* (cf. chapt. 4.1.1.1.). M 11 is inserted on the posterior apophysis of pleopod protopodite IV.

M 13: Arises on the front margin of the large pleotelsonic tergite which is still demarcated by a suture from the pleon tergite III in *Asellus* (cf. chapt. 4.1.1.1.). M 13 is inserted on the posterior apophysis of pleopod protopodite V.

4.2.3.2. Comparison

– Occurrence of the tergal pleopod promotors

As it is the case in the malacostracan groundpattern the pleopods I–V of the Tanaidacea *(Apseudes)* and of some isopodan taxa (e.g. Phreatoicidea, Valvifera

and "Flabellifera") have one extrinsic tergal promotor respectively (cf. ERHARD 1995: 29, 1998a: 32, figs. 13–14). The Asellota obviously have lost all pleopod promotors (figs. 11, 19). Also the Oniscidea lack the promotors Mm 111–114 (pleopods I and III–V). However, the oniscidean tergal promotor M 5 of the pleopod II is still retained and serves mainly as locomotor of the male copulatory organ, the pleopod endopodite II (cf. ERHARD 1995, 1996, 1997, 1998a: fig. 15).
Probably, the reduction of the tergal pleopod promotors in the Oniscidea and Asellota might be convergent features. Provided the reduction of Mm 111–114 in the pleopods I and III–V represents a homologous condition in both groups, a hypothetical last common ancestor of Oniscidea and Asellota must have retained at least the pleopod II promotor M 5 which would have been reduced in the asellotan stemline.

– Origin of the tergal pleopod remotors
In the Tanaidacea *(Apseudes latreillii)* as well as in the Isopoda (e.g. Phreatoicidea, Oniscidea, Valvifera) the tergal remotors Mm 2, 6, 9, 11, 13 within the pleopods I–V originate on the pleon tergites I–V (cf. ERHARD 1998a: figs. 13–15). In the Asellota a corresponding spatial arrangement could be shown for the remotors Mm 2, 6 and 9 within the pleonites I, II and III (figs. 11, 19).
Possibly as a result of the fusion of the pleonites IV–VI and the formation of a pleopodal chamber which is ventrally covered by the pleopod exopodites III, the insertion openings of the pleopods III–V as well as the pleopod protopodites III–V are conspicuously approached in asellotan species (chapt. 4.1.1., figs. 8–9). Presumably, due to this autapomorphous asellotan character state (chapt. 4.1.1.2.) the tergal remotors of the pleopods IV and V have approached the remotor of the pleopod III (figs. 11, 19). Therefore, the remotor of the pleopod IV, M 11, is attached on the pleon tergite III and not on the tergite IV as it is the case in the isopodan groundpattern. Furthermore, the remotor of the pleopod V, M 13, takes its origin at the front margin of the large pleotelson which corresponds to the pleon tergite IV. The forwards directed shift of the muscles Mm 11 and 13 has to be considered an autapomorphous character state of the Asellota.

4.2.4. Pleotelsonic musculature (figs. 10–11, 15)

4.2.4.1. Asellotan species

M 109: The ventral flexor of the pleotelson which is present in the Phreatoicidea and Oniscidea (ERHARD 1998a: figs. 8–10, 13, 16) could not be shown in the investigated asellotan species (figs. 11, 15).

M 110: The muscle lifts the pleotelsonic sternum, enlarges the ventral pleopodal chamber and, probably, stabilizes the large asellotan pleotelson. On both sides within the pleotelson of *Asellus aquaticus* M 110 arises on the pleotelsonic tergite and is inserted on the pleotelsonic sternite (fig. 11). Composed of about 6–8 bundles which are arranged next to each other. Presumably homologous to M 110 of the Phreatoicidea (ERHARD 1998a: 34, figs. 8–9, 13). M 110 could not be shown within the pleotelson of the stenasellids *Protelsonia gjorgjevici* and *Stenasellus costai.*

4.2.4.2. Comparison

– M 109

In the Phreatoicidea the ventral longitudinal muscle M 109 stretches between the cranial and caudal pleotelsonic sternites and works as flexor of the pleotelson (ERHARD 1998a: 34–35, figs. 11, 13). A muscle with a corresponding location could be shown in the basal oniscidean species *Ligia oceanica* (ERHARD 1998a: 35, fig. 16). However, in the investigated asselotan species a homologous branch M 109 does not occur (figs. 11, 15). Further in- and outgroup comparisons are necessary to assess the exact polarity of the different character states.

– M 110

In the Phreatoicidea M 110 is located in the caudal region of the pleotelson. The muscle is composed of numerous bundles, shows a tergosternal pass and flexes as continuation of the ventral longitudinal musculature the phreatoicidean pleotelson (ERHARD 1998a: 34–35, fig. 8). On account of its tergosternal pass and its location between the pleotelsonic tergum and ventrum M 110 of *Asellus aquaticus* (figs. 11, 15) might be homologous to M 110 of the Phreatoicidea. However, the function of M 110 in *Asellus* is different from that in the Phreatoicidea. It does not work as flexor but as levator of the pleotelsonic ventrum and as stabilizer of the large pleotelson. In contrast, a corresponding muscle could not be shown in the Oniscidea (ERHARD 1995, 1996, 1997, 1998a). Further out- and ingroup comparisons might answer the question whether M 110 is present within the isopodan groundpattern.

5. Other anatomical features

5.1. Ventral nerve cord (fig. 20)

Within the phreatoicidean and, presumably, the isopodan groundpatterns the pleonal ganglia of the ventral nerve cord are positioned in a strict metameric pattern:

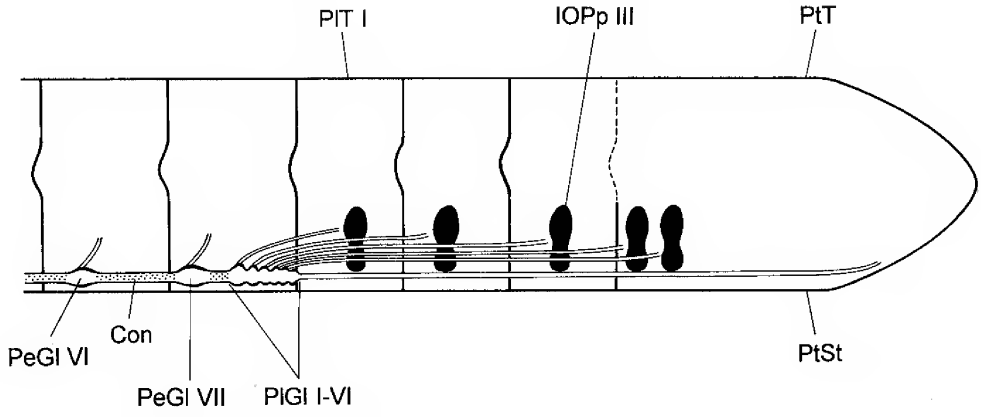


Fig. 20. Diagram showing the position of the ganglia of the ventral nerve cord within the hypothetical groundpattern of the Asellota (compare with corresponding diagram of the Phreatoicidea and Oniscidea in ERHARD 1998a: figs. 17–18).

Each pleon segment bears one pair of ganglia. However, the pleonite V of the Phreatoicidea has incorporated the ganglia of the pleon segment VI which fused with the telson (cf. ERHARD 1998a: fig. 17). The plesiomorphous metameric pattern of ganglia applies also to the presumptive isopodan sistergroup Tanaidacea as it could be shown in the species *Apseudes latreillii* (cf. CLAUS 1887: 12, fig. 12). In the Oniscidea the ancestral state is rather obscured (cf. ERHARD 1998a: fig. 18). All six pairs of pleonal ganglia have been shifted into the pereionite VII and are situated close behind the pereional ganglia VII. The ganglia of the pleon are more or less condensed, innervating the pleonites by long slender nerves. Exactly identical conditions show the ventral nerve cords of *Asellus aquaticus* and *Stenasellus costai* (fig. 20) which was, in the case of *Asellus,* already reported by VANDEL (1943: 107). The pattern of characters reveals the oniscidean and asellotan character states to be apomorphous in respect to the isopodan groundpattern. Probably, the identical transformations in both groups characterize homologous features. However, future anatomical comparisons are necessary to make clear statements.

5.2. Testicular follicles (figs. 21–23)

According to ERHARD (1998a: 37) the number of male testicular follicles per body side in the Phreatoicidea usually differs between 5 and 10. Species of other isopodan groups like the Oniscidea (e.g. *Ligia oceanica,* fig. 21; cf. HEWITT 1907 and MATHUR 1961), Asellota (e.g. *Asellus aquaticus,* fig. 22), Valvifera (e.g. *Saduria entomon,* cf. HRYNIEWIECKA-SZYFTER & TYCZEWSKA 1991: fig. 2) and "Flabellifera" (e.g. *Sphaeroma rugicauda,* cf. ZIMMER 1927: fig. 783) have only 3 testicular lobes per side.

Only few data on the testes in peracaridan outgroups are known: In the species *Apseudes latreillii* of the presumptive isopodan sistergroup Tanaidacea the paired testes are pearshaped organs which are composed of 6 to 10 testicular bodies respectively (fig. 23). ZIMMER (1927) and GRUNER (1993) report on numerous (6–11) spermatic sacs in the mysid taxa *Mysis* and *Neomysis* and of 4 blind-ending testicular lobes in males of the cumacean species *Leucon nasica.* A Mysida-like status with several testicular lobes at the fused cranial ends of the male gonads occurs also in the euphausiacean species *Euphausia superba* (ZIMMER 1927: fig. 888).

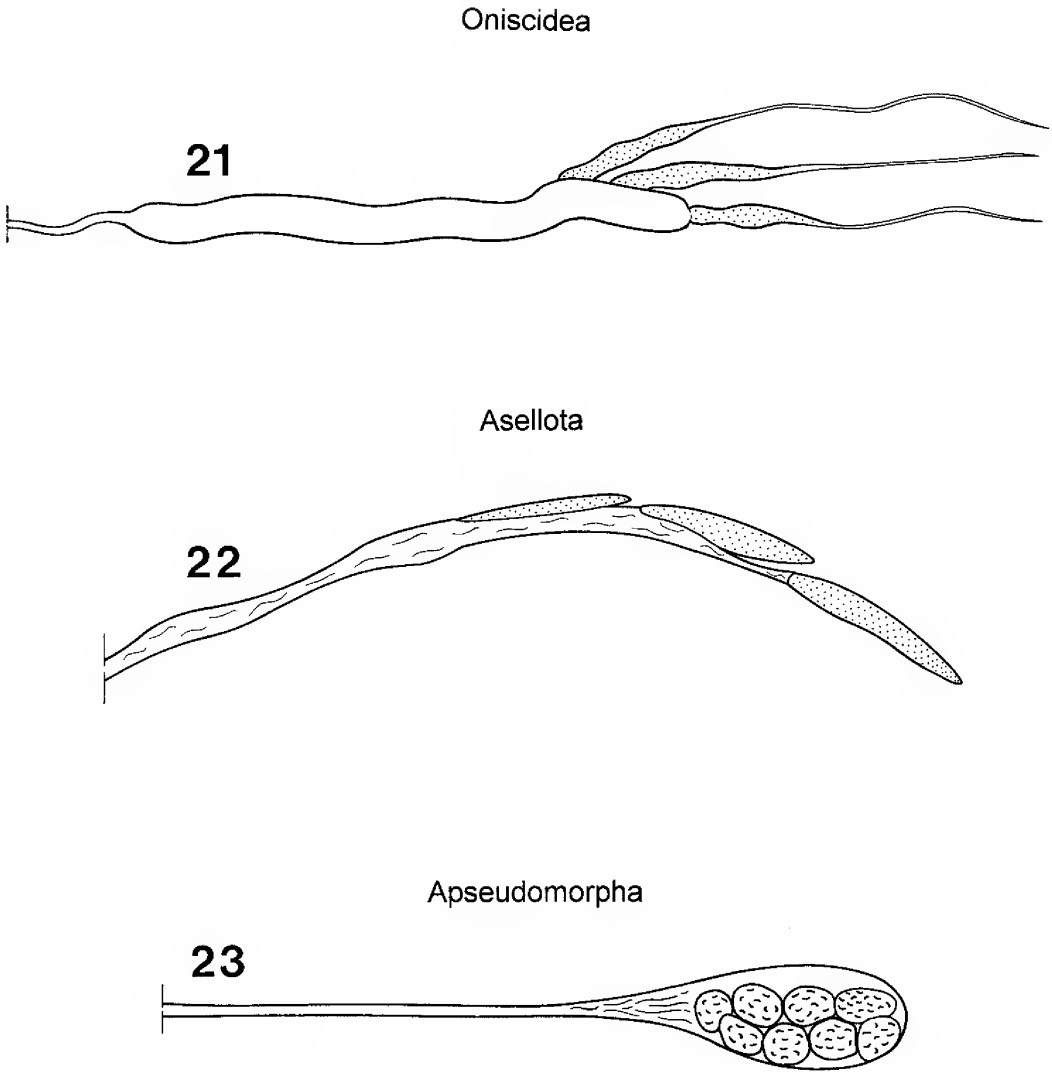
On account of these data the exact determination of the number of testicular follicles within the isopodan groundpattern appears to be difficult. As already mentioned by WÄGELE (1989: 56) the high number of testicular lobes in the Phreatoicidea, probably, might represent a plesiomorphous status and the presence of only 3 follicles could represent an apomorphy of all non-phreatoicidean isopods. However, further anatomical studies are necessary to substantiate or refute this hypothesis.

6. Conclusions

6.1. Groundpattern characters

6.1.1. Pleonal exoskeleton

Long, well developed and separate pleon segments I and II represent a plesiomorphous groundpattern character of the taxon Asellotan while the presence of short



Figs. 21–23. Distal parts of the testes in isopodan and tanaidacean taxa [compare with testes of *Metaphreatoicus australis* (Phreatoicidea) in ERHARD 1998a: fig. 19]. – 21. *Ligia oceanica* (Oniscidea), redrawn after HEWITT (1907); – 22. *Asellus aquaticus* (Asellota); – 23. *Apseudes latreillii* (Tanaidacea), redrawn after CLAUS (1887).

and dorsally fused pleonites I and II is a derived condition of subordinate asellotan groups (chapt. 4.1.1.2.).

The presence of **three separate anterior pleon segments** presumably represents a groundpattern character of the Asellota present for example in *Vermectias* and *Asellus.* The complete fusion of the pleon segments IV, V and the true isopodan pleotelson (pleonite VI + telson) might be an apomorphous status of the Asellota in respect to the isopodan, phreatoicidean and oniscidean groundpatterns (chapt. 4.1.1.2.).

The vaulted pleotelsonic trunk, present within the groundpattern of the Phreatoicidea, might represent a unique apomorphous character of the group while the

slightly dorsoventrally compressed pleotelson of the Asellota, Oniscidea, Calabozoidea, *Tainisopus* and further isopodan groups is assumed to be a plesiomorphous status in respect to the isopodan groundpattern (chapt. 4.1.1.2.).

The presence of long downward developed pleon epimera as part of a specific pleopodal chamber might represent an apomorphous groundpattern character of the Phreatoicidea. Comparable structures are missing in the presumptive isopodan sistergroup Tanaidacea as well as in all non-phreatoicidean isopods (chapt. 4.1.1.2.).

The formation of a protective chamber for the pleopod endopodites III and the pleopods IV–V by the pleopod exopodites III and the pleotelsonic ventrum might be an autapomorphous character state of the Asellota and represents a convergence to the pleopodal chamber of the Phreatoicidea (chapt. 4.1.1.2.).

Within the isopodan and phreatoicidean groundpatterns as well as in *Tainisopus* the male genital papillae arise directly on the medial walls of the pereiopod coxopodites VII. In the asellotan groundpattern the lateral positioned genital papillae arise from sclerites immediately medial to and articulating with the pereiopod coxopodites VII. That situation represents an apomorphous character state in respect to the isopodan and phreatoicidean groundpatterns (chapt. 4.1.1.2.).

Also in the oniscidean groundpattern the genital papillae arise from sclerites of the pereion sternum VII which are connected with the lateral coxal regions. The midventral position of the male genital papillae of the Oniscidea represents an apomorphous status in respect to the isopodan, phreatoicidean and asellotan groundpatterns (chapt. 4.1.1.2.).

6.1.2. Pleonal endoskeleton

"Dorsal apophyses" at the anterior edges of all pleon tergites are present at least in the Phreatoicidea, Oniscidea, Valvifera and "Flabellifera" (Cymothoidae). In the asellotan groundpattern homologous apophyses occur only at the pleon tergites I–III but are missing in the large asellotan pleotelson (pleonites IV–VI + telson) which might represent an apomorphous character state in respect to the isopodan groundpattern (chapt. 4.1.2.2.).

Posterior pleopod protopodite apophyses for the tergal pleopod remotors could be shown so far in the Phreatoicidea, Asellota, Oniscidea, Valvifera and Flabellifera (Cymothoidae). Anterior apophyses for tergal pleopod promotors could only be documented at the pleopod protopodites of the Phreatoicidea and the Valvifera (chapt. 4.1.2.2.).

In the Asellota the male pleopods I and II are positioned close together presumably for the purpose of protection and covering the male gonopods (pleopods II) by the pleopods I. This character state might represent an autapomorphous status of the Asellota (chapt. 4.1.2.2.).

The insertion openings of the pleopods III–V are clearly approached in the investigated asellotan species. Presumably, this features might represent an autapomorphous groundpattern character of the Asellota (chapt. 4.1.2.2.).

6.1.3. Pleonal longitudinal musculature

Within the phreatoicidean and the oniscidean groundpatterns the external layer of the pleonal dorsal longitudinal musculature consists of segmental muscles (Mm

42–46) which are located within the pleonites I–V. In the Asellota only the muscles Mm 42–43 within the pleonites I and II could be shown which might be an autapomorphy of the Asellota (chapt. 4.2.1.1.2).

In the isopodan groundpattern the internal layer of the pleonal dorsal longitudinal musculature (M 41) is running through the entire pleon and is ending on the front margin of pleonite VI (pleotelson). In the Asellota M 41 is inserted already on the front margin of pleonite III which might be an autapomorphous character state (chapt. 4.2.1.1.2.).

On account of the formation of immovable and fused caudal pleonites the muscles Mm 37–39 of the external layer of the ventral longitudinal musculature are completely reduced in the Asellota which might represent an autapomorphous character state (chapt. 4.2.1.1.1.2.).

In the phreatoicidean and isopodan groundpatterns the central layer of the ventral longitudinal musculature is formed by distinct muscle units descending from the tergal front margins of the trunk segments and forming together a compound ventral muscle cord. In the Oniscidea and Asellota the tergosternal and ventral components of the central layer are separated to a great extent and the ventral subunits condensed to a uniform muscle string. The latter condition is assumed to be an apomorphous character state (chapt. 4.2.1.2.2.2.).

In the groundpattern of the Phreatoicidea all tergosternal branches of the pleonal central layer of the ventral longitudinal musculature Mm 3, 7 and 105–108 are present while the Oniscidea and the Asellota have lost the dorsoventral parts of the muscles Mm 105–108 within the pleonites II–V. Additionally, the Asellota have also lost the tergosternal part of M 7 within the pleonite I. The complete reduction of corresponding muscles have to be considered as apomorphous features (chapt. 4.2.1.2.2.2.).

In male specimens of the tanaidacean *Apseudes latreillii* and the isopodan taxon Phreatoicidea the vas deferens runs laterally to the tergosternal part of the ventral longitudinal muscle M 3. In the Oniscidea, Asellota and Valvifera the vas deferens passes between two branches of M 3 which, presumably, represents an apomorphy in respect to the isopodan groundpattern (chapt. 4.2.1.2.2.2.).

The Phreatoicidea and the Oniscidea have one tergosternal component of the internal layer of the ventral longitudinal musculature in all trunk segments. In the Asellota only Mm 1, 4, 8 within pereionite VII and the pleonites I and II could be shown. The reduction of tergosternal components within other trunk segments might be an apomorphous character state in respect to the isopodan groundpattern (chapt. 4.2.1.2.3.2.).

Within the groundpattern of the Isopoda the tergosternal parts of the muscle units of the internal layer of the vLM are directly connected with their ventral prolongations. The retained tergosternal parts Mm 1, 4, 8 in the Asellota and the tergosternal parts Mm 10, 12, 14 in the Oniscidea have lost their connection to the ventral cord which represent different apomorphous character states (chapt. 4.2.1.2.3.2.).

The plesiomorphous type of insertion of the pleonal tergosternal muscle units of the internal layer (Mm 1, 4, 8, 10, 12) is characterized by the attachment on the back margins of pleon sternites still retained in phreatoicidean species. In the Oniscidea and the Asellota the points of insertion of the tergosternal muscle units at the back margins of the pleonites have been shifted forward to the preceding segmental borders which might represent an apomorphous status (chapt. 4.2.1.2.3.2.).

In the Phreatoicidea the ventral parts of the pleonal muscle units of the internal layer of the vLM are still retained as distinct muscle bundles. In the Oniscidea and Asellota these pleonal bundles are condensed to a uniform string which might represent an apomorphous feature in respect to the isopodan groundpattern (chapt. 4.2.1.2.3.2.).

Within the groundpattern of the Isopoda the ventral cord of the internal layer of the vLM is running the entire pleon and is inserted at the pleon sternite VI (pleotelson). In the Asellota the ventral cord is already ending at the pleon sternite IV (asellotan pleotelson) which might be an autapomorphous character of the group (chapt. 4.2.1.2.3.2.).

6.1.4. Stabilizers of the pleonal "dorsal apophyses"

The neighbouring front margins of the lateral pleon tergites ("dorsal apophyses") in the Phreatoicidea and Oniscidea are braced by the horizontal muscles Mm 18–26a. While the muscles Mm 18/19 and 20/21 could be shown in the pleonites I and II of the Asellota the tergite locomotors Mm 22–26a or at least Mm 24–26a have been reduced within the immovable asellotan caudal pleonites. This character state represents an autapomorphy of the Asellota (chapt. 4.2.2.2.).

In the Phreatoicidea the tergite locomotor M 15 is running horizontally between the "dorsal apophyses" of pereion tergite VII and pleon tergite I. In the Oniscidea and Asellota M 15 arises at the mid-region of pereion tergite VII and passes ventrocaudally to the "dorsal apophysis" of pleon tergite I which might be an apomorphous character state in respect to the isopodan groundpattern (chapt. 4.2.2.2.).

In the Phreatoicidea and Oniscidea the stabilizer and locomotor of the pleon tergite I, M 16, is present. A corresponding muscle could not be shown so far in the investigated asellotan species (chapt. 4.2.2.2.).

6.1.5. Extrinsic pleopod locomotors

In the isopodan groundpattern the pleopods I–V each have one extrinsic tergal promotor (Mm 111, 5, 112–114). The Oniscidea have only retained the pleopod II-promotor M 5 while the Asellota obviously have lost all pleopod promotors. The reduction of tergal pleopod promotors has to be considered as an apomorphy (chapt. 4.2.3.2.).

In the Asellota the remotors Mm 11 and 13 of the pleopods IV and V originate on the pleon tergite III and IV while the homologous muscles in the isopodan groundpattern are attached on the pleon tergites IV and V. The character state of the Asellota might represent an autapomorphy of the group (chapt. 4.2.3.2.).

6.1.6. Pleotelsonic musculature

In the Phreatoicidea and Oniscidea the ventral longitudinal pleotelsonic muscle M 109 is present while in the Asellota a homologous branch does not occur (chapt. 4.2.4.2.).

In the Phreatoicidea as well as in the Asellota the tergosternal pleotelsonic muscle M 110 is present while in the Oniscidea a corresponding muscle could not be shown (chapt. 4.2.4.2.).

6.1.7. Other anatomical features

In the tanaidacean, isopodan and phreatoicidean groundpatterns the pleonal ganglia of the ventral nerve cord are positioned in a strict metameric pattern. In the Oniscidea and Asellota all six pairs of pleonal ganglia have been shifted into the pereionite VII which represent apomorphous charater states in respect to the isopodan groundpattern (chapt. 5.1.).

6.2. Apomorphies

Within part 1 of the present publication series (ERHARD 1998a: 39) some presumptive apomorphous characters as well as anatomical features with uncertain polarity of the phreatoicidean and oniscidean pleon trunk are listed. The paper in hand provides further information on the anatomy of the pleon trunk especially of the taxon Asellota. These new data supplement the knowledge on the pleonal anatomy of the above mentioned isopodan groups and reveal further presumptive apomorphies in respect to the isopodan groundpattern which are described below.

It is emphasized that these new results only can represent the current state of knowledge. A final and comprehensive phylogenetical analysis of the pleonal characters described within the parts 1–4 of this publication series will be mainly the subject of a following fifth paper. This will include further in- and outgroup comparisons and a detailed discussion of the phylogenetic relationships of the taxa Phreatoicidea, Oniscidea, Asellota and further isopodan groups.

6.2.1. Phreatoicidea

Presumptive autapomorphies of the Phreatoicidea which might substantiate the monophyly of the group are the presence of a vaulted pleotelsonic trunk (chapt. 4.1.1.2.) and the formation of a ventral pleopodal chamber by downward developed pleon epimera, anterior lateroventral pleotelsonic extensions, laterally flattened uropod protopodites, the dorsally curved pleotelsonic apex as well as the adjacent regions of the caudal pleotelsonic margin (chapt. 4.1.1.2.).

6.2.2. Oniscidea/Asellota

The following presumptive apomorphies in respect to the isopodan groundpattern are present in the oniscidean as well as in the asellotan groundpattern. It has to be checked by further ingroup comparisons whether these derived characters occur also in other isopodan groups: The medially directed shift of the male genital papillae from the pereiopod coxopodites VII onto a sclerite of the pereion sternite VII (chapt. 4.1.1.2.), the condensation of the ventral muscle units of the central layer of the ventral longitudinal musculature (vLM) and the separation from their tergosternal components (chapt. 4.2.1.2.2.2.), the complete reduction of the tergosternal branches of Mm 105–108 (central layer of the vLM) within the pleonites II–V (chapt. 4.2.1.2.2.2.), the intermuscular pass of the male vas deferens between two branches of the ventral longitudinal muscle M 3 (chapt. 4.2.1.2.2.2.), the forward directed shift of the insertion points of the tergosternal muscle units of the pleonal internal layer of the ventral longitudinal musculature (chapt. 4.2.1.2.3.2.), the condensation of the pleonal ventral parts of the internal layer of the vLM forming a uniform

ventral muscle cord (chapt. 4.2.1.2.3.2.), the apomorphous pass of the pleon tergite I-locomotor M 15 (chapt. 4.2.2.2.) and the presence of all six pleonal ganglia of the ventral nerve cord within the pereionite VII (chapt. 5.1.).

6.2.3. Oniscidea

The presence of the following presumptive apomorphies of the Oniscidea in other isopodan taxa still has to be checked by further ingroup comparisons: The mid-ventral position of the paired male genital papillae on a sclerite of the pereionite VII (chapt. 4.1.1.2.), the separation of the tergosternal muscle components Mm 10, 12 and 14 from their ventral parts of the internal layer of the vLM (chapt. 4.2.1.2.3.2.) as well as the reduction of the extrinsic pleopod promotors Mm 111–114 within the pleopods I and III–V (chapt. 4.2.3.2.).

6.2.4. Asellota

Presumptive autapomorphies of the Asellota which might substantiate the monophyly of the group are the presence of a large pleotelson formed by the complete fusion of the pleonites IV–VI and the telson (chapt. 4.1.1.2.), the operculate pleopod exopodites III forming together with the pleonal ventrum a protected chamber for the pleopod endopodites III and the pleopods IV–V (chapt. 4.1.1.2.), the lack of "dorsal apophyses" as points of muscular attachment within the fused pleonites IV–VI (chapt. 4.1.2.2.), the approachment of the male pleopods I and II (chapt. 4.1.2.2.), the approachment of the insertion openings of the pleopods III–V (chapt. 4.1.2.2.), the complete reduction of the caudal branches of the external layer (Mm 44–46) and the internal layer (M 41) of the pleonal dorsal longitudinal musculature (chapt. 4.2.1.1.2.), the lack of the muscles Mm 37–39 of the external layer of the pleonal ventral longitudinal musculature (chapt. 4.2.1.1.1.2.), the complete reduction of the ventral cord of the internal layer of the vLM between pleonite IV and VI (chapt. 4.2.1.2.3.2.), the lack of the caudal pleon tergite stabilizers and locomotors Mm 22–26a (chapt. 4.2.2.1.) and the forwards directed shift of the attachment points of the tergal remotors Mm 11 and 13 of the pleopods IV and V to the pleon tergites III and IV (chapt. 4.2.3.2.).

The presence of following presumptive apomorphies of the Asellota in other isopodan taxa still has to be checked by further ingroup comparisons: The complete reduction of the tergosternal part of M 7 within the pleonite I (chapt. 4.2.1.2.2.2.), the reduction of the tergosternal components of the internal layer of the vLM in all trunk segments except pereionite VII and the pleonites I and II (chapt. 4.2.1.2.3.2.), the separation of the retained tergosternal muscle components Mm 1, 4, 8 from their ventral parts of the internal layer of the vLM (chapt. 4.2.1.2.3.2.), the reduction of all extrinsic pleopod promotors Mm 111, 5, 112–114 within the pleopods I–V (chapt. 4.2.3.2.) and the lack of the locomotor and stabilizer of the pleon tergite I, M 16, and its serial homologa within the pereion (chapt. 4.2.2.2.).

6.2.5. Characters of uncertain polarity

In case of several characters of the phreatoicidean, oniscidean and asellotan pleon trunk the polarity of the different states still has to be determined by in- and out-

group comparisons. These characters concern the presence of the ventral longitudinal pleotelsonic muscle M 109 in the Phreatoicidea and Oniscidea and the absence of a corresponding branch in the Asellota (chapt. 4.2.4.2.) as well as the occurrence of the tergosternal pleotelsonic muscle M 110 in the Phreatoicidea and Asellota and its lack in oniscidean species (chapt. 4.2.4.2.).

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8. References

Brusca, R. C. & Wilson, G. D. F. (1991): A phylogenetic analysis of the Isopoda with some classificatory recommendations. – Mem. Queensld Mus. **31**: 143–204; Brisbane.

Cannon, H. G. (1937): A new biological stain for general purposes. – Nature **139**: 549; London.

Claus, C. (1887): Ueber *Apseudes latreillii* Edw. und die Tanaiden. II. – Arb. zool. Inst. Univ. Wien **7**: 139–220; Vienna.

Erhard, F. (1995): Vergleichende- und funktionell-anatomische Untersuchungen am Pleon der Oniscidea (Crustacea, Isopoda). Zugleich ein Beitrag zur phylogenetischen Systematik der Landasseln. – Zoologica **145**: 1–114; Stuttgart.

– (1996): Das pleonale Skelet-Muskel-System und die phylogenetisch-systematische Stellung der Familie Mesoniscidae (Isopoda: Oniscidea). – Stuttgarter Beitr. Naturk. (A) **538**: 1–40; Stuttgart.

– (1997): Das pleonale Skelet-Muskel-System von *Titanethes albus* (Synocheta) und weiterer Taxa der Oniscidea (Isopoda), mit Schlußfolgerungen zur Phylogenie der Landasseln. – Stuttgarter Beitr. Naturk. (A) **550**: 1–70; Stuttgart.

– (1998a): Morphological and phylogenetical studies in the Isopoda (Crustacea). Part 1: The pleon trunk in the Phreatoicidea. – Stuttgarter Beitr. Naturk. (A) **581**: 1–42; Stuttgart.

– (1998b): Phylogenetic relationships within the Oniscidea (Crustacea, Isopoda). – Isr. J. Zool. **44**: 303–309; Jerusalem.

– (1999): Morphological and phylogenetical studies in the Isopoda (Crustacea). Part 2: The pleopods and uropods in the Phreatoicidea. – Stuttgarter Beitr. Naturk. (A) **597**: 1–56; Stuttgart.

– (2001): Morphological and phylogenetical studies in the Isopoda (Crustacea). Part 4: The pleopods and uropods in the Asellota. – Stuttgarter Beitr. Naturk. (A) **624**: 1–51; Stuttgart.

Gruner, H.-E. (1953): Der Rollmechanismus bei kugelnden Landisopoden und Diplopoden. – Mitt. zool. Mus. Berlin **29**: 148–179; Berlin.

– (1993): Crustacea. – *In:* Kaestner, A.: Lehrbuch der Speziellen Zoologie 1, Teil 4: Arthropoda (ohne Insecta): 448–1030; Jena, Stuttgart & New York (G. Fischer Verlag).

Hennig, W. (1966): Phylogenetic systematics. – 263 pp.; Urbana, Chicago & London (Univ. Illinois Press).

Hewitt, C. G. (1907): *Ligia.* – Proc. Trans. Liverpool biol. Soc. **21**: 65–100; Liverpool.

Hryniewiecka-Szyfter, Z. & Tyczewska, J. (1991): The histology of the male reproductive system of *Saduria entomon* (Linnaeus, 1758) (Isopoda, Valvifera). – Crustaceana **60**: 246–257; Leiden.

Just, J. & Poore, G. C. B. (1992): Vermectiadidae, a new primitive asellote isopod family with important phylogenetic implications. – J. crust. Biol. **12**: 125–144; Lawrence.

KOBUSCH, W. (1999): The phylogeny of the Peracarida (Crustacea, Malacostraca). Morphological investigations of peracaridan foreguts, their phylogenetic implications, and an analysis of peracaridan characters. – Vol. **1** & **2**: 277 pp.; Göttingen (Cuvillier Verlag).

KRAUTER, D. (1980): Ein rasch arbeitendes, schonendes Mazerationsmittel für Chitinpräparate: Diäthylentriamin. – Mikrokosmos **69**: 395–397; Stuttgart.

KUSSAKIN, O. G. (1973): Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep-sea fauna origin. – Mar. Biol. **23**: 19–34; Berlin.

MAERCKS, H. H. (1930): Sexualbiologische Studien an *Asellus aquaticus* L. – Zool. Jb. (Abt. Physiol.) **48**: 399–508; Jena.

MATHUR, R. S. (1961): The male genitalia of *Oniscus asellus* (Linnaeus). – J. Roy. micr. Soc. **80**: 9–17; London.

SCHMALFUSS, H. (1989): Phylogenetics in Oniscidea. – Monitore zool. ital. (N. S.) (Monogr.) **4**: 3–27; Florence.

SEROV, P. A. & WILSON, G. D. F. (1995): A review of the Stenetriidae (Crustacea: Isopoda: Asellota). – Rec. Aust. Mus. **47**: 39–82; Sydney.

SIEG, J. (1984): Neuere Erkenntnisse zum natürlichen System der Tanaidacea. – Zoologica **136**: 1–132; Stuttgart.

SKET, B. (1985): A contribution to the general morphology of Protojaniridae (Isopoda, Asellota) with some phylogenetic considerations concerning Asellota. – Crustaceana **48**: 200–208; Leiden.

TABACARU, I. & DANIELOPOL, D. L. (1999): Contribution à la connaissance de la phylogénie des Isopoda (Crustacea). – Vie Milieu **49**: 163–176; Banyuls-sur-Mer.

VAN LIESHOUT, S. E. N. (1983): Calabozoidea, a new suborder of stygobiont Isopoda, discovered in Venezuela. – Bijdr. Dierk. **53**: 165–177; Leiden.

VANDEL, A. (1943): Essai sur l'origine, l'évolution et la classification des Oniscidea (isopodes terrestres). – Bull. biol. Fr. Belg. (Suppl.) **30**: 1–136; Paris.

WÄGELE, J.-W. (1982): On a new *Microcerberus* from the Red Sea and the relationship of the Microcerberidea to the Anthuridea (Crustacea, Isopoda). – Zool. Scr. **11**: 281–286; Oxford.

– (1983): On the origin of the Microcerberidae (Crustacea: Isopoda). – Z. zool. Syst. Evolut.-Forsch. **21**: 249–262; Hamburg & Berlin.

– (1989): Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. – Zoologica **140**: 1–262; Stuttgart.

WILSON, G. D. F. (1987): The road to the Janiroidea: Comparative morphology and evolution of the asellote isopod crustaceans. – Z. zool. Syst. Evolut.-Forsch. **25**: 257–280; Hamburg & Berlin.

– (1994): A phylogenetic analysis of the isopod family Janiridae (Crustacea). – Invertebr. Taxon. **8**: 749–766; Melbourne.

WILSON, G. D. F. & KEABLE, S. J. (in press): Systematics of the Phreatoicidea. – Submitted, Crustacean Issues Series; Rotterdam (A. A. Balkema).

WILSON, G. D. F. & PONDER, W. F. (1992): Extraordinary new subterranean isopods (Peracarida: Crustacea) from the Kimberley Region, Western Australia. – Rec. Aust. Mus. **44**: 279–298; Sydney.

WILSON, G. D. F. & WÄGELE, J.-W. (1994): Review of the family Janiridae (Crustacea: Isopoda: Asellota). – Invertebr. Taxon. **8**: 683–747; Melbourne.

WOLFF, T. (1962): The systematics and biology of bathyal and abyssal Isopoda Asellota. – Galathea Rep. **6**: 1–320; Copenhagen.

ZIMMER, C. (1927): Mysidacea, Cumacea, Tanaidacea, Isopoda & Euphausiacea. – *In:* KÜKENTHAL, W. & KRUMBACH, T. (eds.): KÜKENTHALS Handbuch der Zoologie **3**, Teil 1: 607–766, 812–839; Berlin & Leipzig (Walter de Gruyter & Co).

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